AURORA TORRES MORENO - 2016 PHD THESIS

PHD THESIS

WILDLIFE IN A HUMAN-DOMINATED WORLD:

impacts of anthropogenic landscape changes on birds and mammals in Spain

AURORA TORRES MORENO - *2016*

La vida animal en un planeta humanizado: *efectos sobre aves y mamíferos de los cambios en el paisaje producidos por el hombre en España.*

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Nota acerca del idioma:

En la redacción de la presente tesis doctoral se han utilizado dos idiomas: español e inglés. Los apartados *Introducción, Justificación, estructura y objetivos de la tesis* y *Síntesis general* han sido escritos en castellano, mientras que los Capítulos 1–4 aparecen íntegramente en inglés (idioma original en el que fueron redactadas las investigaciones para su posterior publicación en revistas científicas internacionales). Se incluyen en ambos idiomas los siguientes apartados: *Contenidos*, *Resumen de la tesis*, *Resumen de los Capítulos 1–4* y *Conclusiones*.

Note about the language:

This PhD Thesis has been written in two languages: Spanish and English. *Introduction, Rationale, Structure, and Objectives*, and *General Synthesis* has been written in Spanish, while *Chapters 1-4* are entirely in English (language in which the research were written for publication in international scientific journals). The following sections are included in both languages: *Contents*, *Abstract*, *Rationale, Structure, and Objectives*, *Abstracts of the Chapters 1-4,* and *Conclusions*.

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Wildlife in a human-dominated world: impacts of anthropogenic landscape changes on birds and mammals in Spain

La vida animal en un planeta humanizado: efectos sobre aves y mamíferos de los cambios en el paisaje producidos por el hombre en España

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A mis padres
y mis abuelas

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"… After all, ecology is just about 'everything'."
(a few minutes before he called us to action using an old hunting horn)

John A. Wiens keynote during the banquet
at IALE World Congress in Landscape Ecology
Portland July 8th 2015

CONTENTS
Contenidos

THESIS ABSTRACT 13
Resumen de la tesis

ABBREVIATIONS 17
Abreviaturas

INTRODUCTION 19
Introducción

Theoretical background
Antecedentes y estado actual del tema

Thesis Rationale, Structure, and Objectives
Justificación, estructura y objetivo de la tesis

References
Referencias

CHAPTER 1. Assessing the effects of a highway on a threatened species using Before–During–After & Before–During–After-Control–Impact designs 41

CHAPTER 2. Large-scale wildlife responses to human structures: A novel approach to assessing the impact of infrastructural development 75

CHAPTER 3. Multi-scale mismatches between urban sprawl and landscape fragmentation create windows of opportunity for conservation development 105

CHAPTER 4. Time-lags in farmland bird responses to landscape and climate changes 163

General synthesis and perspectives 211
Síntesis general y perspectivas

Conclusions 225
Conclusiones

Acknowledgements 229
Agradecimientos

Thesis abstract

As a result of the age-old co-evolution between farming systems and natural habitats in the Mediterranean basin, the agricultural landscapes harbour an extraordinary amount of biodiversity. However, farmland is today the habitat in Europe with the highest proportion of bird species with unfavourable conservation status. Agricultural intensification is considered responsible for the negative trends of biodiversity in farmlands. But we live on a human-dominated planet, and during the last decades other drivers of landscape change have also been operating and extending across the Mediterranean basin at an unprecedented rate. The aim of this PhD thesis is to analyse the influence of intensive land-uses – namely, infrastructural development, urban sprawl, and agricultural intensification – on Mediterranean landscapes and wildlife populations, with a special focus on farmland birds. The studies comprising this PhD dissertation illustrate the process that led me to address this challenge.

I started my PhD working on the effects of road building on a population of an emblematic bird of agricultural landscapes, the Great bustard (*Otis tarda*), in central Spain (**Chapter 1**). I analysed changes in its spatial distribution and population trends before, during, and after the construction of a road in areas close to the road and far away. I found solid evidence for effects of the road construction on the great bustard population, including avoidance behaviour and declining population trends. Based on this work it was imperative to further study the relevance of the negative effects of this and other type of infrastructure on wildlife populations in agricultural landscapes.

Despite the ubiquity of human infrastructure, few attempts have been made to spatially quantify their impact at large scales. In **Chapter 2**, I show an analysis of the pervasiveness of European transportation infrastructure. Highlighting the Spanish case, I present a novel method for assessing the spatial extent of the impacts from infrastructure on wildlife populations at large scales, based on taxa-specific functional distance-decay response curves. I revealed both the pervasiveness of human infrastructure and its potential to negatively influence wildlife populations, particularly of wide-ranging mammals. In addition, farmlands turned out to be the habitat most exposed to both transportation infrastructure and built-up areas, and therefore where the strongest effects of infrastructure are predicted.

One of the most widely recognized effects of human infrastructure is landscape fragmentation. Landscape fragmentation patterns are commonly assumed to be strongly correlated to other drivers of environmental change like urban sprawl, representing a growing threat to biodiversity. In **Chapter 3**, I test the hypothesis that sprawl and fragmentation patterns strongly match, based on spatially explicit quantifications of urban sprawl and landscape fragmentation gradients in Spain. I conclude that the sprawl-fragmentation relationship does not prevail, is non-stationary, and depends on scale. Thus, the assessment of the impact of intensive land-uses should report on both with separate indicators.

In light of these insights, I developed a landscape experiment in the Iberian Peninsula, in which I quantify the changes in agricultural intensification, landscape fragmentation and urban sprawl in the last sixty years, controlling by the effect of climate change and the cultivated area (**Chapter 4**). These changes can cause immediate loss of species but also time-delayed extinctions. In this study, I found strong evidence for time-lagged responses in the farmland bird community. Present-day richness of species is better explained by past predictors of the landscape and the climate. A time-lag in the habitat breadth of the bird community is less clear. The major predictors for present-day richness of species were the degree of urban dispersion and the mean temperature in the past, which affected negatively the richness. However, habitat breadth of the bird community was better explained by agricultural intensification and landscape fragmentation. Conservation decisions in agricultural landscapes based on the analysis of how species respond to present-day landscapes and only focused on agricultural intensification are likely insufficient to prevent the species loss in the future.

Resumen de la tesis

Debido a la antigua coevolución entre los sistemas agrarios y los hábitats naturales en la cuenca mediterránea, los paisajes agrícolas albergan una gran biodiversidad. Sin embargo, las zonas agrícolas son hoy el día el hábitat con la mayor proporción de especies de aves con un estado de conservación desfavorable. Se considera que el principal responsable de estas tendencias negativas es la intensificación agrícola. No obstante, vivimos en un planeta dominado por humanos y durante las últimas décadas también han operado a una velocidad sin precedentes otras fuerzas impulsoras de cambios en el paisaje. El objetivo de esta tesis doctoral es analizar la influencia de los usos intensivos del suelo – específicamente el desarrollo de infraestructuras, la expansión urbanística y la intensificación agrícola – en los paisajes mediterráneos y en las poblaciones de animales salvajes, con especial interés en las aves asociadas a medios agrícolas. Los estudios que componen esta tesis doctoral muestran el proceso que me llevó a abordar este desafío.

Comencé mi doctorado trabajando en los efectos de la construcción de una autopista en una especie emblemática de medios agrarario, la Avutarda común (*Otis tarda*), en el centro peninsular (**Capítulo 1**). Analicé los cambios en su distribución espacial y sus tendencias poblacionales antes, durante y después de la construcción de la infraestructura en áreas cercanas a la ésta y en zonas alejadas. Encontré evidencias sólidas de los efectos negativos de la construcción de la autopista en la población de Avutardas, incluyendo un comportamiento elusivo y tendencias poblacionales descendentes. A partir de este trabajo fue imperativo avanzar en el estudio de la importancia de los efectos negativos de estas y otras infraestructuras en las poblaciones de fauna salvaje de los paisajes agrícolas.

A pesar de lo ubicuo de las infraestructuras humanas, se han llevado a cabo pocos intentos de cuantificar espacialmente su impacto a gran escala. En el **Capítulo 2**, muestro un análisis de proximidad a las infraestructuras europeas de transporte. Destacando el caso de España, presento un método novedoso para evaluar la extensión espacial a gran escala de los impactos de infraestructuras en poblaciones salvajes, basándome en curvas de disminución la de respuesta específicas de taxones. Los resultados revelan la omnipresencia de las infraestructuras humanas así como su potencial para influir negativamente sobre las poblaciones de animales silvestres, sobre todo

los de mamíferos con grandes áreas de campeo. Además, las zonas agrícolas resultaron ser los hábitat más expuestos tanto a las infraestructuras de transporte como a las edificaciones y, por tanto, donde se predicen los efectos más importantes de las infraestructuras.

Uno de los efectos más ampliamente reconocidos de las infraestructuras humanas es la fragmentación del paisaje. Normalmente se asume que los patrones de fragmentación del paisaje están muy correlacionados con otros factores que producen cambios ambientales como la dispersión urbanística, representando una amenaza creciente para la biodiversidad. En el **Capítulo 3**, testo la hipótesis de que la dispersión urbanística y los patrones de fragmentación están fuertemente correlacionados basándome en cuantificaciones explícitas de dispersión urbanística y de fragmentación en España. Concluyo aquí que la relación dispersión-fragmentación no es predominante, varía a través del espacio y con la escala. Por lo tanto, la evaluación del impacto de usos intensivos del suelo debe informar de ambos aspectos empleando distintos indicadores.

A la luz de estas ideas, desarrollo un experimento de paisaje en la península ibérica, en el que cuantifico los cambios en intensificación agrícola, fragmentación del paisaje y dispersión urbanística en los últimos sesenta años controlando el efecto del cambio climático y la superficie cultivada (**Capítulo 4**). Estos cambios pueden conducir a una pérdida inmediata de especies, pero también extinciones con un cierto retraso temporal. En este estudio encuentro evidencias considerables de retrasos en las respuesta de las comunidades de aves de medios agrícolas. La riqueza actual de especies se explica mejor con variables predictivas del pasado, tanto del paisaje como del clima. No está tan claro el retraso temporal en el nivel de amplitud de habitat de la comunidad. Los mejores predictores de la riqueza resultaron ser el grado de dispersión urbanística y la temperatura media en el pasado, que afectaron negativamente a la riqueza. Sin embargo, el nivel de amplitud de hábitat de la comunidad se relacionó con la intensificación agrícola y la fragmentación del paisaje. Por tanto, las decisiones referentes a la conservación en paisajes agrícolas basados en cómo responden las especies a paisajes actuales y enfocados exclusivamente en la intensificación agrícola son probablemente insuficientes para evitar la pérdida de especies en el futuro.

ABBREVIATIONS

Abreviaturas

AP: Relación Área-perímetro (*Area-to-Perimeter ratio*)
BA: Antes-Después (*Before-After*)
BACI: Antes-Después-Control-Impacto (*Before-After-Control-Impact*)
BCN: Base cartográfica nacional
BDA: Antes-Durante-Después (*Before-During-After*)
BDACI: Antes-Durante-Después-Control-Impacto
(*Before-After-During Control-Impact*)
CI: Control-Impacto (*Control-Impact*)
CLC: Corine Land Cover
DIS: Grado de dispersión urbanística (*Degree of urban dispersion*)
GIS: Sistema de Información Geográfica (*Geographic Information System*)
GWR: Regresión ponderada geográficamente
(*Geographically Weighted Regression*)
HB: Amplitud de hábitat (*Habitat breadth*)
HP: Horizonte de percepción (*Horizon of perception*)
IPCC: Panel Intergubernamental de Cambio Climático
(*Intergovernmental Panel on Climate Change*)
m_{eff}: Tamaño de malla eficaz (*Effective mesh density*)
MSA: Índice de abudancia media de especies (*Mean Species Abundance index*)
OLS: Regresión lineal de mínimos cuadrados ordinarios
(*Ordinary Least-Square Regression*)
PC: Percentage of croplands
PUA: Proporción de superficie urbana (*Proportion of urban area*)
s_{eff}: Densidad de malla eficaz (*Effective mesh density*)
SIOSE: Sistema de Información sobre Ocupación del Suelo de España
UP: Grado de penetración urbana (*Degree of urban permeation*)
UPU: Unidades de penetración urbana (*Urban permeation units*)

Introduction

Introducción

Antecedentes y estado actual del tema

Transiciones agrícolas y urbanización

Hace entre 300 y 400 generaciones, la especie humana pasó de ser cazadora/recolectora a cultivar sus propios alimentos (Diamond 2002). Esto supuso la transición del '*nature use*' al '*land use*', una manera totalmente diferente de relacionarse con el ambiente (Haber 2007) y un punto y aparte en la historia de la humanidad. Desde entonces, el ser humano ha ido alterando los ecosistemas conforme a sus necesidades (demandas de alimentos, fibra, agua, etc.) a costa del ambiente del resto de organismos en el planeta.

La naturaleza, que había sido el suporte de la vida de los humanos en planeta durante muchos milenios, se convertía en su competidor, amenazando a las cosechas y al ganado o tratando de reconquistar lo que los agricultores habían arrebatado (Haber 2007). En todos los lenguajes aparecieron nuevas palabras como "mala hierba", "plaga" ó "alimaña". A pesar de ello los cultivos agrícolas tuvieron gran éxito. Poco después, el cultivo de grano (cereal) permitía obtener copiosas cosechas que podían ser almacenadas y transportadas. Más y más agricultores producían cantidades de alimento que excedían sus necesidades de autoconsumo. Con el crecimiento en la producción de alimentos y el progreso tecnológico de la Edad de los Metales la población creció considerablemente. Con el excedente de los agricultores llegaron los "no agricultores", que formaron asentamientos donde se concentraba la población.

Esos "no-agricultores" crearon el modo de vida urbano y se hicieron cargo del desarrollo de la cultura y la civilización, aunque seguían dependiendo de lo que producían los agricultores. La humanidad, que hasta entonces estaba, dentro de las diferentes culturas, bastante homogéneamente estructurada, se dividió entonces en "rural" y "urbana". La rama urbana creció en poder, influencia y conocimiento, dejando a los agricultores atrás. La importancia ecológica del alimento quedó a la sombra de su importancia económica y su valor monetario (Haber 2007). La presión por los recursos se incrementó de nuevo de forma substancial. El abastecimiento de recursos de los ecosistemas locales no podía responder a la demanda de una creciente población, lo que resultó en una ampliación de la extensión geográfica para demanda y suministro de recursos (upscaling). Esta tendencia se reforzó con el desarrollo de infraestructuras y medios de transporte y con la demanda de productos exóticos (e.g., especias y metales preciosos), de una población que crecía y se enriquecía aumentando el consumo de recursos. Con ello, la huella ecológica de la sociedad aumentaba (Luck et al. 2001). La dependencia de los ecosistemas se hacía cada vez menos obvia y decaía el estatus de los que extraían recursos de los ecosistemas (e.g., agricultores, pescadores o leñadores) (Cumming et al. 2014).

A finales del s. XVIII se abría la puerta a los avances tecnológicos modernos, con la explotación de energías fósiles. En los países desarrollados, las zonas rurales se iban vaciando de la que gente que se marchaba a las zonas urbanas buscando mejores oportunidades. Cada vez había menos agricultores y más gente a la que alimentar, por tanto se hacía necesario incrementar el rendimiento de los cultivos. El rudimentario instrumental de los agricultores tenía que ser reemplazado por potentes máquinas que funcionaran con combustibles fósiles, haciendo la dura faena del agricultor mucho más cómoda. Además las tierras de cultivo se podían expandir a zonas donde antes no se podía cultivar. La aplicación de estiércol fue reemplazada por la fácil utilización de fertilizantes sintéticos. El uso de pesticidas sintéticos hizo más sencilla la pelea contra las malas hierbas y las plagas. Estos cambios resultaron en una agricultura moderna basada en combustibles fósiles. Estos avances incrementaron y estabilizaron el suministro de alimentos. Sin embargo este progreso de la agricultura se ha visto ensombrecido por los numerosos efectos perjudiciales de los productos químicos, especialmente a medida que se aplican en cantidades excesivas para obtener cada vez mayores rendimientos e ingresos (Haber 2007). Otra consecuencia de este proceso ha sido la dramática simplificación de los paisajes agrícolas, ya que los campos de cultivo se han adaptado a la nueva maquinaria, eliminando pequeños elementos del paisaje (bordes, árboles aislados, estanques e incluso edificaciones), que contribuían enormemente a la biodiversidad de estos sistemas (Suárez et al. 1997; Stoate et al. 2009). Más aún, las concentraciones parcelarias han homogeneizado el mosaico agrario y actuado en detrimento de las especies que se benefician de la variedad de hábitat. Además, cada vez una parte mayor de la cosecha se utiliza para alimentar al ganado que ha ido ganando peso en nuestra dieta. De hecho, en 2011 se estima que el 75% de la superficie agrícola (cultivos y pastos) se dedicó a la producción animal (Foley et al. 2011).

Haber (2007) propone que estos cambios han resultado en un patrón de usos del suelo que comprende seis tipos: (1) producción de alimentos, (2) producción de otros recursos de origen biológico (fibras, madera o combustible), (3) construcción de edificios o infraestructuras de transporte, (4) extracción de recursos no biológicos (grava, arena, arcilla) y almacenamiento de residuos, (5) amenidad, recreación y placer y (6) conservación y protección de la naturaleza. Todas estos usos compiten por el suelo y hacen que sea un recurso cada vez más escaso (Foley et al. 2005; Haber 2007).

Estos usos del suelo están interrelacionados y la secuencia conlleva una serie de reglas: (i) cada uso produce al siguiente, (ii) el siguiente influye sobre todos sus predecesores y (iii) cada uso del suelo produce nuevas – y más o menos irreversibles – condiciones ambientales. La agricultura es tanto el primer con el como el último uso del suelo, porque todos los otros usos dependen de él. Si la agricultura desapareciera o no fuera posible el resto de usos desaparecerían. Por la tanto, los paisajes agrícolas, su distribución, y en especial los que la gestionan merecen la atención prioritaria de la sociedad (Haber 2007).

La gran aceleración. el problema del cambio global

Durante el mismo periodo en el que se ha producido la intensificación agrícola, otros procesos de cambio global han modificado sustancialmente los paisajes. A mediados del s. XX se produce un cambio brusco en la magnitud y la velocidad en la que las actividades humanas impactan sobre el planeta (Fig. 1), que se acelera desde entonces (Steffen et al. 2004; Steffen et al. 2015). De hecho, algunos autores denominan a este momento como "la gran aceleración" y entienden que es único en la historia de la humanidad (The great acceleration; Steffen et al. 2004).

Esta tendencia es especialmente notoria para el desarrollo de zonas urbanas e infraestructuras de transporte (Fig. 1). Lejos de detenerse, se espera que la urbanización se incremente del 52% en 2011 al 67% o más en 2050 (UNPD 2012). La creciente urbanización y la demanda cada vez mayor de recursos, irán de la mano con el desarrollo de infraestructuras de transporte, transformando los paisajes a escala global (Grimm et al. 2008; Seto et al. 2012). Este desarrollo conlleva una serie de impactos: el mayor uso per cápita de la energía, el incremento de emisiones de gases de efecto invernadero, la liberación de carbono almacenado en forma de biomasa vegetal, niveles superiores de contaminación, la pérdida de suelo, la intensificación de los incendios o la pérdida de terreno cultivable, entre otros (Newman & Kenworthy 1999; Imhoff et al. 2004; Spyratos et al. 2007; Scalenghe & Marsan 2009; Churkina et al. 2010). Se espera que estos cambios ambientales aceleren la extinción de especies, la homogeneización de las comunidades bióticas, la

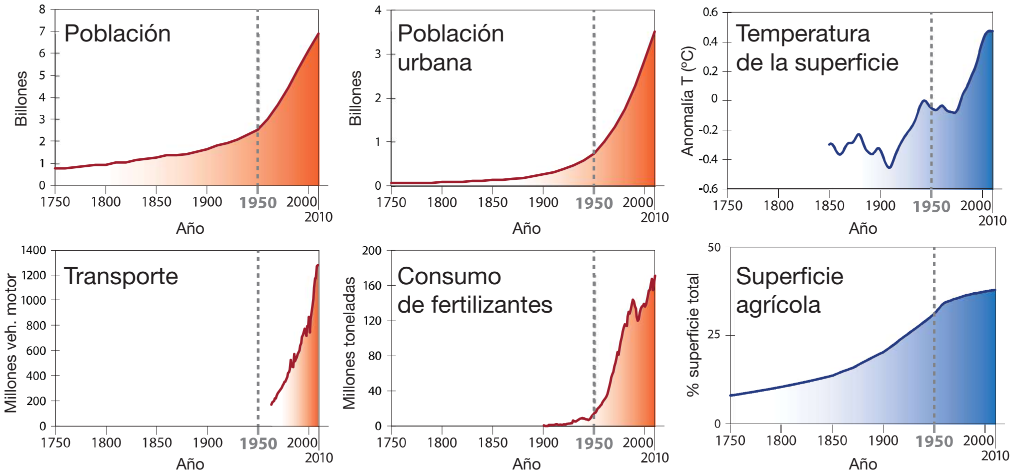

Figura 1. Tendencia de 1750 a 2010 en indicadores agregados globalmente de desarrollo socio-económicos (en rojo) y de la estructura y funcionamiento de la Tierra (en azul) (Steffen et al. 2015). (1) Datos de la población mundial según la base de datos HYDE, (2) Incremento mundial de vehículos a motor por año. De 1963 a 1999 los datos incluyen coches de pasajeros, autobuses, vehículos de transporte, tractores, camionetas, camiones, motocicletas y ciclomotores. Datos de 2000 a 2009 incluyen coches, autobuses, camiones, camionetas y motocicletas, (3) Datos mundiales de población urbana según la base de datos HYDE. Los datos anteriores a 1950 han sido modelados. Los datos están representados como puntos por década, (4) Consumo mundial de fertilizantes (nitrógeno, fosfato y potasio) según datos de la International Ferlizer Industry Association (IFA), (5) Anomalía de la temperatura de la superficie a escala global (HadCRUT4: combinación de observaciones para la tierra y los océanos, relativo a 1961-1990, suavizado con un modelo gausiano a 20 años), y (6) Incremento de la superficie agrícola, considerando pastos y cultivos como porcentaje de la superficie total.

introducción y dispersión de especies invasoras, así como plagas (Forman et al. 2003; Hanski 2005; Devictor et al. 2007; Hahs et al. 2009; Dirzo et al. 2014).

Lejos de concentrarse el desarrollo en los núcleos urbanos, la dispersión urbanística (*urban sprawl* en inglés) se ha ido haciendo cada vez más común y no sólo ha estado limitada las zonas metropolitanas (Brown et al. 2005; EEA 2006; Inostroza et al. 2013). Un número cada vez mayor de investigaciones sobre los efectos de distintos patrones de desarrollo urbano en poblaciones de fauna – particularmente en aves – indican que los patrones con baja dispersión, es decir, compactos, reducen los efectos negativos sobre la abundancia de las poblaciones (McDonnell & Hahs 2008; Gagné & Fahrig 2010). A lo largo de esta tesis se considera que las unidades de estudio se sitúan a lo largo de un gradiente continuo de dispersión urbanística, en vez categorizarla y diferenciar entre dispersión urbanística de las ciudades (*urban sprawl*) y de los pueblos (*rural sprawl*).

Los asentamientos humanos junto a las vías de comunicación son los principales lugares desde los que se origina la pérdida de hábitat y su deterioro, las amenazas más importantes para la biodiversidad global (Dirzo et al. 2014; WWF 2014). Aunque estas infraestructuras pueden tener efectos positivos sobre algunas especies, la mayor parte de los efectos detectados son negativos (revisado por Fahrig & Rytwinski 2009). En las últimas décadas, las agencias de transporte se han hecho cada vez más conscientes de los efectos de carreteras, ferrocarriles y otras infraestructuras en la fauna (Forman & Alexander 1998; Trombulak & Frissell 2000). Y es que cada vez es mayor la evidencia de que las infraestructuras reducen las poblaciones de muchas especies mediante (i) incrementos de la mortalidad, (ii) pérdida y deterioro del hábitat y (iii) fragmentación de poblaciones en subpoblaciones más pequeñas, con el consiguiente riesgo de extinción local (Forman et al. 2003; Fahrig & Rytwinski 2009 para carreteras).

Uno de los principales efectos del desarrollo de infraestructuras es la fragmentación del paisaje. Este proceso da lugar a tres cambios principales en la estructura de paisaje: (i) un incremento del aislamiento de los parches naturales (o semi-naturales), (ii) un incremento del número de parches y de la longitud de bordes y (iii) un descenso del tamaño promedio de los parches (Fahrig 2003). Los cambios en la estructura del paisaje resultan en una distribución discontinua de las especies, lo que supone una inmigración reducida y una mayor vulnerabilidad a procesos de extinción local (Fischer & Lindenmayer 2007). De forma simultánea al proceso de fragmentación del paisaje, la conectividad entre las estructuras humanas puede verse notablemente incrementada, lo que supone mayores posibilidades de dispersión para las especies que utilizan esos espacios del paisaje (Watling et al. 2011), así como para las especies invasoras (Crowl et al. 2008).

Por tanto, los efectos de las infraestructuras, incluyendo carreteras, no se limitan exclusivamente a la superficie ocupada o junto a la infraestructura, sino que se extienden hasta distancias variables desde la infraestructura, incluso varios kilómetros (Benítez-López et al. 2010). El área sobre la que se extienden los efectos ecológicos producidos por la infraestructura es el área de influencia de la infraestructura (en el caso de carreteras '*Road-Effect Zone*'; Forman & Deblinger 2000). Como consecuencia, las redes de infraestructuras pueden poner en peligro la persistencia a largo plazo de las poblaciones de fauna silvestre, las comunidades y los ecosistemas (Fahrig & Rytwinski 2009; Benítez-López et al. 2010; Borda-de-Água et al. 2011; Kociolek et al. 2011).

A los cambios en el paisaje se unen los cambios en clima. La temperatura del planeta se ha incrementado durante el último siglo (en 0.7 ºC; IPCC 2007), y particularmente en las últimas tres décadas (Fig. 1; Karl & Trenberth 2003). Los efectos del calentamiento incluyen, entre otros, cambios en la distribución de especies, sus abundancias y fenología (Parmesan 2006; Lenoir & Svenning 2013; Pavón-Jordán et al. 2015). Por ello el cambio climático es una reconocida amenaza para la fauna (Thomas 2011).

Los profundos cambios ambientales derivados de estas actividades humanas y sus interacciones plantean nuevos interrogantes sobre la respuesta de las especies ante el cambio global (Brook et al. 2008), y su estudio constituye una línea de investigación clave en ecología del paisaje (*Landscape Ecology*; Turner 2005).

Los paisajes agrícolas mediterráneos y sus aves

En la cuenca Mediterránea se crearon paisajes agrícolas a expensas de deforestaciones con el fin de aumentar los terrenos cultivables, y se han mantenido con un manejo tradicional durante miles de años (Blondel & Aronson 1999). Como resultado de esta larga co-evolución entre sistemas agrícolas y las especies silvestres, estos sistemas acabaron sosteniendo una elevada biodiversidad beneficiando incluso a algunas especies (Ruiz 1990; Tucker et al. 1994; Farina 1997; Blondel & Aronson 1999).

En la actualidad, la superficie labrada cubre casi un tercio de la superficie en España (30.5%; MARM, 2009) y los aprovechamientos agrarios en su conjunto abarcan la mitad del territorio (50.3%; MARM, 2009). Los medios agrarios albergan una gran proporción de la biodiversidad europea, por ejemplo, más del 50% de todas las especies de aves de la UE (Pain & Pienkowski 1997; EEA 2005). En la península ibérica, muchas de las aves ligadas a medios agrícolas son especies genuinamente esteparias (Fig. 2). Estas especies han ido adaptándose de las estepas naturales a las zonas agrícolas de secano, con las que guardan gran similitud estructural: paisajes abiertos y con escasa vegetación arbórea (Suárez et al. 1992; Santos & Suárez 2005). Se trata de aves

Figura 2. Muestra de aves características de paisajes agrícolas en la península ibérica. De izquierda a derecha y de arriba a abajo: Alondra común (*Alauda arvensis*), Aguilucho cenizo (*Circus pygargus*), Ganga ortega (*Pterocles orientalis*), Sisón común (*Tetrax tetrax*), Avutarda común (*Otis tarda*) y buitrón (*Cisticola juncidis*).

propias de espacios abiertos, que nidifican y se alimentan en el suelo, y que presentan una serie de adaptaciones comunes (De Juana 2005).
Desde mediados del s. XX, se han venido registrando tendencias negativas en las aves ligadas a medios agrarios en toda Europa. Esto las ha convertido en el grupo de aves más amenazado en esta región (PECBMS 2009). El declive poblacional se ha relacionado principalmente con la fuerte intensificación de la agricultura desde hace por lo menos tres décadas (Donald et al. 2001; Robinson & Sutherland 2002). No obstante, la construcción de carreteras y edificaciones también han sido identificadas como causes de pérdida y deterioro del hábitat (Boutin & Métais 1995; Silva et al. 2004; Santos & Suárez 2005).

Justificación, estructura y objetivos de la tesis

Justificación

Como se ha visto a lo largo de la introducción, desde mediados del siglo XX y con mayor intensidad en las últimas décadas, están teniendo lugar procesos de cambio en el paisaje y en el clima a una velocidad sin precedentes (Steffen et al. 2015). Estos procesos ejercen fuertes presiones sobre la fauna, las comunidades y los ecosistemas y abren nuevas incógnitas sobre su capacidad de respuesta. En las últimas décadas, el conocimiento de cada uno de estos procesos ha experimentado un notable avances. Sin embargo, son muchos aún los interrogantes sobre (i) los efectos de las infraestructuras a gran escala y la cuantificación de su área de influencia (van der Ree et al. 2011; van der Ree et al. 2015), (ii) las relaciones teóricas y empíricas entre distintos procesos de cambio (Brook et al. 2008), y (iii) la contribución de cambios ambientales en paisajes agrícolas – más allá de la intensificación agraria – al declive de la biodiversidad asociada a estos medios.

Estructura de la tesis

En la presente tesis doctoral se abordan estas cuestiones mediante estudios en un orden secuencial, por el que los resultados de una investigación conducen a la siguiente para finalmente abordar el último de los interrogantes. En este proceso se abordan distintas escalas y se utilizan aproximaciones orientadas a especies y a patrones, pues ambas son complementarias para entender la ecología de los paisajes modificados (Fischer & Lindenmayer 2007). Además, se proponen medidas concretas en apoyo de la conservación y la planificación. La tesis comienza con un enfoque orientado a una especie concreta (‘species-oriented’), la Avutarda común, una especie emblemática de paisajes agrícolas (Capítulo 1). Luego se centra en los taxones de aves y mamíferos para cuantificar el área de influencia de infraestructuras en estos grupos (Capítulo 2). Finalmente pasamos a enfocarnos en patrones de paisaje y su relación con medidas de presencia de especies (‘patterns-oriented’), incluyendo medidas agregadas como la riqueza de especies o indicadores funcionales como la amplitud de hábitat (Capítulos 3 y 4).

Objetivo general Analizar la influencia de los usos intensivos del suelo – concretamente el desarrollo de infraestructuras, la dispersión urbanística y la intensificación agraria – sobre los paisajes mediterráneos y la fauna, con especial interés en las aves de medios agrícolas.

Main objective To analyse the influence of intensive land-uses – namely, infrastructural development, urban sprawl, and agricultural intensification – on Mediterranean landscapes and wildlife populations, with a special focus on farmland birds.

Objetivos específicos

1 Investigar los efectos de la construcción de una infraestructura lineal de transporte en una población de avutardas. (Capítulo 1)

- Comprobar si la especie muestra un comportamiento elusivo y cuantificar distancias umbral a la infraestructura.
- Examinar los efectos en las tendencias poblacionales.
- Analizar los efectos sobre la productividad.

2 Analizar la ubicuidad de infraestructuras. (Capítulo 2)

- Cuantificar la ubicuidad de las infraestructuras lineales de transporte en Europa.
- Cuantificar la ubicuidad de las infraestructuras lineales de transporte, edificaciones y otras infraestructuras en España.
- Explorar los efectos de la ubicuidad de las infraestructuras en la distribución de especies.

3 Plantear un enfoque para estimar el área de influencia de infraestructuras para poblaciones de aves y mamíferos a escala regional o nacional. (Capítulo 2)

- Estimar el área de influencia de las infraestructuras para las poblaciones de aves y mamíferos en España.

4 Investigar la interacción entre los patrones de fragmentación del paisaje y los patrones de dispersión de la urbanización a múltiples escalas en España. (Capítulo 3)

- Analizar el grado de congruencia entre los patrones de fragmentación de paisaje y los patrones de dispersión urbanística.
- Determinar si el signo y la magnitud de esa relación varía a través del espacio.
- Analizar el efecto de la escala sobre dicha relación.
- Ampliar el marco conceptual de la relación entre los patrones de desarrollo de infraestructuras de transporte y los de dispersión urbanística.

5 Investigar si la comunidad de aves de paisajes agrícolas mediterráneos responde de forma inmediata o con cierto retraso a los cambios ambientales. (Capítulo 4)

- Analizar si la riqueza actual de especies se explica mejor por valores actuales o por valores pasados de paisaje y clima.
- Analizar si la diversidad funcional de la comunidad se explica mejor por valores actuales o por valores pasados de paisaje y clima.

6 Investigar influencia relativa de la intensificación agrícola, la dispersión urbanística, la fragmentación del paisaje y el cambio climático en las comunidades de aves de medios agrícolas mediterráneos. (Capítulo 4)

- Analizar la influencia relativa de estos factores sobre la riqueza actual de especies.
- Analizar la influencia relativa de estos factores sobre la amplitud de hábitat de la comunidad.

Contribución original de la doctoranda

Esta tesis ha producido cuatro artículos originales de investigación. El Capítulo 1 ya se encuentra publicado en *Biological Conservation*, mientras que los Capítulos 2 y 3 están en proceso de revisión en *Conservation Letters* y *Landscape Ecology* respectivamente. Finalmente, el Capítulo 4 se haya en fase de preparación. He contribuido a la concepción y diseño de estos trabajos, la recolección y el análisis de los datos, la discusión de los resultados y he liderado la redacción de todos los manuscritos.

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Chapter

Capítulo

Evaluando los efectos de una autovía en una especie amenazada mediante diseños BDA y BDACI

Resumen

Debido a una mayor concienciación sobre impacto potencial de las carreteras, los gestores demandan estudios bien diseñados sobre las implicaciones de las infraestructuras lineales en los ecosistemas. En este estudio, ilustramos la aplicación de diseños Antes-Durante-Después y Antes-Durante-Después-Control (BDA y BACI respectivamente) para evaluar los efectos de la construcción de autopistas y su funcionamiento usando como modelo una población de Avutarda común (*Otis tarda*). Basándonos en una serie temporal demográfica (1997-2009) y en datos de distribución, desarrollamos modelos aditivos generalizados y árboles de clasificación para testar el efecto de la distancia a carreteras en la distribución de las avutardas, identificar la distancia de impacto de las carreteras y explorar la estacionalidad de estos efectos. Se seleccionaron dos zonas control para evaluar los cambios entre las fases de construcción en la productividad y las tendencias poblacionales usando modelos TRIM. Desde el principio de la construcción de la vía, las avutardas tendieron a evitar la cercanía a la autopista (ca. 560-750 m de distancia límite). La banda de exclusión fue más estrecha durante la época reproductiva. Además, los grupos familiares fueron menos tolerantes a las molestias causadas por el uso de la autopista, como muestra su mayor distancia de efecto (ca. 1300 m). No hubo diferencias en las tendencias poblacionales entre las zonas de impacto y control durante la construcción. Sin embargo, una vez la autopista fue puesta en funcionamiento, el número de avutardas decreció gradualmente hasta un 50% en la zona de impacto, se mantuvo estable en las zona control más cercana y aumentó en la zona control localizada a mayor distancia de la autopista. El efecto en la densidad de grupos familiares fue menos evidente. Nuestro enfoque proporciona información relevante para la conservación de la avutarda y sugiere métodos para obtener información de interés para los gestores de carreteras, que puede aplicarse a infraestructuras lineales con otras especies.

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Assessing the effects of a highway on a threatened species using Before-During-After and Before-During-After-Control-Impact designs

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Abstract

Due to the growing awareness of potential impacts of roads, managers demand well-designed studies about the implications of linear infrastructures on ecosystems. We illustrate the application of before-during-after and before-during-after-control-impact designs (BDA and BDACI) to assess effects of highway construction and operation using a population of great bustards (*Otis tarda*) as a model. Based on a time series of demographic and distribution data (1997-2009), we developed generalized additive models and classification trees to test the effect of road distance on bustard distribution, identify road-effect distances and explore the seasonality of these effects. Two control zones were selected to test the changes between construction phases on productivity, and population trends using TRIM models. From the start of the road construction, great bustards tended to avoid close proximity to the highway (ca. 560-750 m threshold distance). The exclusion band was narrower during the breeding season. In addition, family groups were less tolerant to highway operation disturbances, as shown by their higher distance effect (ca. 1300 m). Population trends did not differ between impact and control zones during the construction. However, once the highway was in operation, bustard numbers declined gradually up to 50% in the impact zone, remained stable in the closest control zone, and increased in the zone located at the greatest distance from the highway. The effects on density of family groups were less evident. Our approach provides information relevant to great bustard conservation and suggests methods for obtaining information of interest to road managers, that could be applied to linear infrastructures with others species.

KEYWORDS Avoidance behaviour, BACI designs, impact assessment, road ecology, road effects, steppe birds.

Introduction

Population growth and increasing demands for connectivity among human settlements have created a huge transport network, with a total length of current roads exceeding 69 million km worldwide (CIA, 2009). Roads are recognized as pervasive vectors of landscape change (Forman et al., 2003), and their impacts on wildlife are a major concern for managers, who are in need of reliable information to support their conservation decisions (e.g., Ament et al., 2008). As a consequence, the study of road effects on biological diversity and ecological processes has grown recently (e.g., Balkenhol and Waits, 2009; Coffin, 2007; Fahrig and Rytwinski, 2009), creating a new scientific discipline called road ecology (Forman, 1998).

Roads usually have profound edge and road-zone effects on habitat quality (Forman and Deblinger, 2000; Reijnen et al., 1996). Even though not all species are equally affected by roads, their presence usually implies some degree of habitat fragmentation (Jaeger et al., 2007), with short or long-term changes in spatial distribution (Pruett et al., 2009) and demographic structure (Tanner and Perry, 2007) of wildlife populations. These changes may eventually affect their genetic diversity and viability (Clark et al., 2009; Epps et al., 2005).

Several methods have been suggested to detect impact of human infrastructures or activities on the environment and on wildlife populations (e.g., Green, 1979; Stewart-Oaten et al., 1986; Wiens and Parker, 1995). One of the most powerful tools is the Before-After-Control-Impact (BACI) design, which uses sampling at control and impact zones through time to provide replication within the "before" and "after" periods (Stewart-Oaten et al., 1986). This approach is widely used in the environmental monitoring literature, to evaluate impacts of temporal activities (e.g., diving: Claudet et al., 2010; hunting: Czetwertynski et al., 2007) or permanent structures (e.g., wind farms: De Lucas et al., 2005; hydroelectric reservoirs: Nellemann et al., 2003), as well as to estimate ecological outcomes of habitat restoration (e.g., Geraldi et al., 2009; Pabian and Brittingham, 2007). BACI design can be applied to a high diversity of organisms, and enables the exploration of a variety of responses, such as changes in abundance, diversity, biomass or body condition. Compared to Control-Impact (CI) or Before-After (BA), the BACI design reduces the effects of temporal and spatial variation by subtracting out naturally varying temporal effects. This is a key advantage, as one of the main practical problems of detecting human influence on population abundances is the large temporal variance of many populations (Underwood et al., 1994).

Despite the potential power and usefulness of BACI designs there are very few published examples for roads (e.g., Chen et al., 2009; Hedrick et al., 2010), because of the need for repetitive sampling over a long period of time, which is expensive and difficult to achieve. Since long-term data series are usually missing, studies typically compare numbers and distributions of the species between impact and control areas once the road causing the impact has been constructed. This method, albeit useful in revealing important information, has important weaknesses that may bring into question the strength of the results (Fahrig and Rytwinski, 2009). Therefore, there remains an urgent need for well-designed studies of road effects on wildlife populations, which can be used to support decision-making during infrastructure planning (Benítez-López et al., 2010; Fahrig and Rytwinski, 2009; Roedenbeck et al., 2007). We used Before-During-After and Before-During-After-Control-Impact designs (BDA and BDACI; Roedenbeck et al., 2007), which also consider potential effects during infrastructure construction. Monitoring populations through the construction period increases our knowledge about effects occurring specifically during this phase, and disappearing once the infrastructure is completed, e.g., effects caused by earthworks, noise or other disturbances caused by trucks.

The primary aim of this study was to apply BACI designs to detect and assess the effects of highway construction on wildlife. As a model species we used the great bustard Otis tarda, a globally threatened steppe bird inhabiting farmland habitats and suffering severe population declines in recent decades partly due to infrastructure development (IUCN, 2010). Agro-steppes host many other endangered species that have been affected by both agricultural intensification and infrastructure expansion (Sanderson et al., 2002; Wretenberg et al., 2007). Steppe birds are indeed at present the most threatened bird group, with 83% of the species subject to unfavorable status (BirdLife International, 2004; Donald et al., 2006). Therefore, understanding the response of steppe wildlife to road construction may facilitate conservation decisions, an issue of growing concern for managers (Santos and Suárez, 2005). Our previous records on numbers and distribution of great bustards in the study area represent a unique opportunity to examine road impacts, since the possibility of assessing populations prior, during and after road development is rare. Specifically, we focused our research on two classical road effects. (1) Changes in the spatial distribution of bustard flocks. We determined road-effect distances through the identification of threshold distances to the highway indicating changes in bird abundance. We also assessed the seasonality of road-effect distances and the differences in avoidance behaviour of flocks and families. (2) Changes in population dynamics in areas near the highway. We tested whether highway construction induced changes in population trends and productivity in impact and control areas. The demographic and spatial data were collected during three time periods (13 years) at three zones. Our results indicate solid evidence for behavioural changes in a bird species due to a new road. In addition, this research provides relevant information and useful recommendations for the impact assessment of road developments, as well as for the management of the species studied.

Materials and methods

Study species

The great bustard is one of the heaviest flying birds (Alonso et al., 2009). It is adapted to pseudo-steppes of cereal farmland, which currently constitute its main habitat in Europe through its whole distribution range, from the Iberian Peninsula to China. Spain is home to 60-70% of this species' world population (Alonso and Palacín, 2010). In spring males gather at traditional lek sites where they display to attract females for mating. Females nest at variable distances from the lek where they mated, and take over all brood-rearing duties. The chicks hatch by early June and follow their mothers during their first 6-18 months of life. During their first summer young birds are vulnerable to predators, and thus families show an elusive behaviour and tend to remain isolated from flocks of non-breeders. In the study area the species behaves as partial and differential migrants between breeding and post-breeding areas (Palacín et al., 2009). Great bustards are relatively long-lived (unpublished data), and show a poor capability to colonize new areas due to their marked philopatry, lek- and nest-site fidelity, and conspecific attraction (Alonso et al., 2004).

Study area and design

The study was carried out in central Spain, at two connected Special Protection Areas for birds (SPA; European Natura 2000 Network; European Commission 2000) "Estepas cerealistas de los ríos Jarama y Henares" and

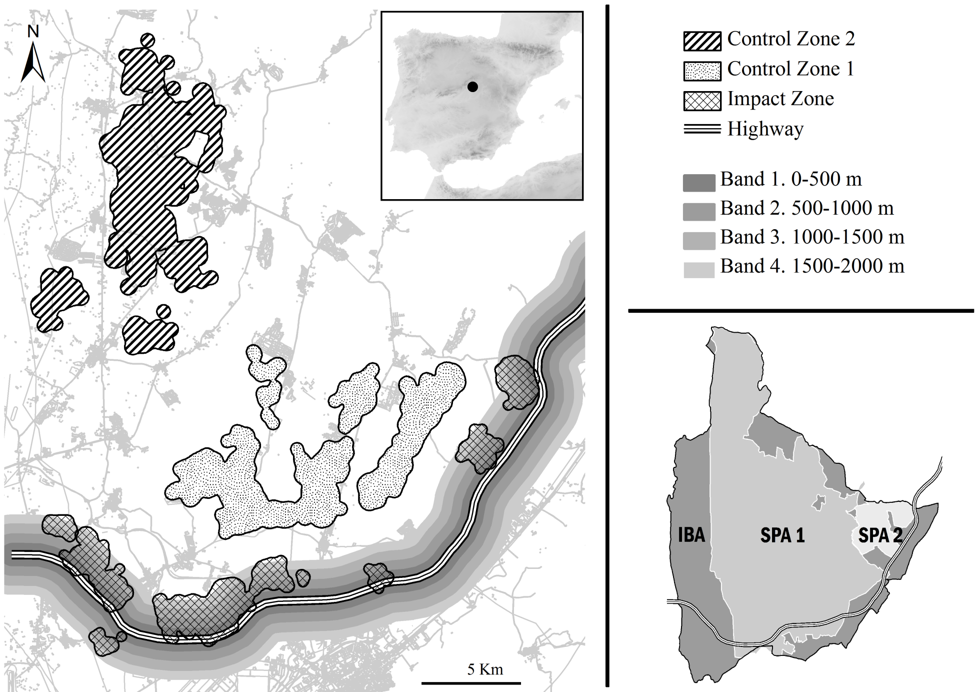

Figure 1. Location of the study area in the Iberian Peninsula showing the impact and control zones of the effects of the highway construction, calculated through a 99% Kernel of all great bustard flocks observed during 1997-2009. The bands around the highway used to analyze the distance effect (see text) are also shown. The figure at the bottom right shows the main protected zones in the study area: "Estepas cerealistas de los ríos Jarama y Henares" (Special Protection Area for birds; SPA 1), "Estepas cerealistas de la Campiña" (SPA 2) and "Talamanca-Camarma" (Important Bird Area; IBA).

"Estepas cerealistas de la Campiña", contained in the Important Bird Area (IBA) "Talamanca-Camarma" (40ºN 3ºW, 520 km^2, 792 a.s.l.; Fig. 1). This region is mainly agro-steppe landscape with a Mediterranean semiarid climate, dominated by extensive cereal (wheat and barley) cultures, and smaller patches of olive groves and legumes. It includes 16 villages and several small developments, with a relatively homogeneous size (mostly 50-250 pop/km^2). Due to its bird richness this area has been classified as a steppe bird "hotspot" in the Iberian Peninsula (Traba et al., 2007).

In October 2001 the construction of the Radial 2 (R2) four-lane highway began in the study area, to join the capital city of Madrid with Guadalajara. For this study we selected the 34 km highway sector that crosses both SPAs. The total amount of earth moved during this period was around 9720 000 m3. Inaugurated in October 2003, the traffic-volume is currently ca. 9500 vehicles/day with a traffic speed limit of 120 km/hour (75 mph). Highway is not associated with any major natural barrier (e.g., mountain or river), is mostly hidden (through noise barriers or embankments) and fenced externally throughout its length.

To explore the changes in the distribution pattern of flocks-to-highway distances we applied a BDA design. We restricted the impact assessment to a 2 km buffer zone from the road, which falls within the reported road-effect distances for most published bird datasets (0-2580 m, Benítez-López et al., 2010; see Pruett et al., 2009 for other lekking birds). Road effect distances were analyzed using two approaches: as a continuous variable within the 2 km buffer, and dividing the buffer zone into four 500 m-wide bands (Fig. 1). For other analyses focused on population trends we applied a BDACI design, keeping the 2 km buffer as the impact zone (IZ).

Regarding the control zones, it is recommended that an intermediate zone be left between control and impact zones (e.g., Bro et al., 2004; Reijnen and Foppen, 1994), just as the monitoring of multiple control, ideally both near and far from the location of the intervention (Conquest, 2000). Thus, we chose a control zone located at more than 2 km from IZ and 7 km from the highway (CZ1; Euclidean distance was calculated to the centroid of the zone). Further and separate from CZ1 we chose another control zone (CZ2, located at 20 km from the highway and at a minimum distance of 10 km from IZ; Euclidean distance was calculated to the centroid of the zone). The habitat in both CZs was similar to that in the IZ, and the birds of all three zones belong to the same population, as concluded from radio-tracking and genetic studies (Alonso et al., 2004; Martín et al., 2002; Martín, 2008). The average bird abundances before highway construction were 251.5 (SD = 68.8) in the IZ, 195.5 (SD = 28.7) in CZ1, and 346.7 (SD = 50.3) in CZ2.

Landscape was relatively stable during the study period, except for the construction of the Radial 2 highway. We measured land-use change from 2000 to 2006 using CORINE Land Cover Changes 2000-2006 map (EEA, 2010), to confirm the low level of land use changes in the zones (2.6% in the impact zone, and 0% and 0.5% in the two control zones). Moreover, the length of roads other than R2 did not increase in any zone during the study period.

Bird surveys

Data were obtained from 49 censuses carried out by the same observers and using the same methodology, in 1997-2009. Each census was conducted by two or three teams of two people each, following pre-established itineraries with four-wheel drive vehicles and stopping frequently to scan for birds with binoculars and telescopes 20-60x. All great bustard flocks were mapped on 1:25 000 topographical maps. The censuses were done almost simultaneously within a year, thus minimizing the risk of double-counting individuals. Also, some birds were previously marked and we could identify the specific groups they belonged to. The total sample recorded was 1517 flocks (15 689 individuals). The first year was omitted in the analyses of demographic processes because the survey was incomplete in the control zones. We defined four seasons: winter (December to January), to provide the amount and distribution of wintering birds; spring (March, when the largest aggregations of individuals at lek sites, i.e., areas for male exhibition and mating, occur), to estimate the number of breeding individuals; early summer (July, when chicks are younger than two months and still following the females), to provide the amount and distribution of birds in summer; late summer (September), when the chicks have overcome the period of highest mortality, to give a second and more reliable estimate of the number of family groups, which by then are more visible.

Distances to highway analyses

We used the Euclidean distance to measure the distance to the highway from the locations of flocks, rather than those of individuals, because in gregarious species the behaviour of each individual in a flock is not independent from that of flock mates. Before carrying out the analyses we tested that there were no significant differences in mean number of bustards per flock among bands or construction phases (respectively, $H = 3.642$, $P = 0.162$, and $H = 5.046$, $P = 0.168$; Kruskal-Wallis test).

We explored distance effects considering three time scales: 1) whole year, based on all census observations, 2) seasonal, selecting the observations for each season, and 3) family groups in late summer. In the latter, we decided to use only family group observations to check whether their response was different, as a consequence of their particular ecological needs. We first aggregated the observations by bands to determine the spatial distribution along the highway, and to assess the possible changes between the three study phases: before, during and after construction of the highway (respectively, 1997-2001, 2001-2003, and 2003-2009). We constructed histograms for every phase with the relative frequency of observations aggregated by bands, and we evaluated the differences with $\chi 2$ tests (Rcmdr package). All statistical analyses were done in R 2.10.1 statistical software (R Development Core Team, 2009).

In addition, we considered distance as a continuous variable and built Generalized Additive Models (GAMs; Hastie and Tibshirani, 1990) with flock presence/pseudo-absence as the response variable and distance to highway as a predictor variable using binomial error structure and logit link. These models served to predict the species probability of presence according to the distance to the highway. The pseudo-absences were obtained from a map of potential habitat for the species, based on all census and sampling observations (Wisz and Guisan, 2009). First, we estimated the home range of great bustards following the cross-validated fixed kernel method (Seaman and Powell, 1997), using Hawth's Tools extension (Beyer, 2004) in ArcGIS 9.2 (ESRI). We defined the home range as the smallest area containing 99% of the observations. Next, in that area we subtracted the surfaces of buildings prior to highway construction. Then, we obtained the same number of random pseudo-absence points as presences (keeping equal weights on the presence and pseudo-absence data sets), applying a 100 m exclusion buffer (see Morales et al., 2008 for little bustard *Tetrax tetrax*) around each observation in order to minimize the probability that great bustards were using those parts of the territory. We created three univariate models, one for each phase, with smoothing splines of distance as the single nonparametric predictor (mgcv package; Wood, 2008).

Classification trees were built for presence/pseudo-absence of flocks with distance to road as a predictor variable (Rpart package), to determine the existence of threshold distances to highway (e.g., Palomino and Carrascal, 2007; Seoane et al., 2009), i.e., distances from the highway at which the probability of species presence increases substantially. These trees are nonparametric, hierarchical classifiers that predict class membership by recursively partitioning a data set into more homogeneous subsets (Breiman et al., 1984). In order to avoid excessively complex models and overfitting, different pruning procedures were performed to better generalize the predictive ability of the tree. Pruning was achieved 1) by eliminating nodes that increase errors in prediction within the pruning data set, 2) by statistically significant reductions of the group heterogeneity after each subdivision, and 3) by limiting the size of the tree to a maximum of six leaves (terminal tips). To evaluate the predictive ability we used the Correct Classification Rate (CCR; Fielding and Bell, 1997) to the whole tree, and the Negative Predictive Power (NPP; Fielding and Bell, 1997) to the first splitting criteria, which identifies the threshold distance.

BDACI analysis of population trends

To detect potential changes in population trends in the study area as a result of the highway construction, we analyzed the annual censuses of the bustard breeding population (March) during 1998-2009 with TRIM software (Pannekoek et al., 2005). TRIM computes population indexes that represent between-year changes, using 1998 as the base year. TRIM analyzes time series of counts using Poisson regression and accounts for overdispersion and temporal autocorrelation of data by estimating log-linear models with generalized estimating equations (e.g., Seoane and Carrascal, 2008; Wretenberg et al., 2007). TRIM models can take into account “change points”, i.e., years when the overall trend of a series changes, and allow testing trends before and after particular change points. TRIM can also consider ’categorical covariates’, i.e., factors that group individual sites on the basis of a feature hypothesized to affect population trends. To test whether population trends differed among phases we divided the data into the same three phases (i.e., 1998-2001, ‘before’; 2002-2003, ‘during’; and 2004-2009 ‘after’). Thus, years 1998, 2001 and 2003 were used as change points in linear (switching) trend models. We also considered ’zone’ covariates as a factor with three levels to test whether population trends differed between impact (IZ) and control zones (CZ1 and CZ2). The Wald statistic (Harrell, 2001) was used to test the change points and covariate significance.

This resulted in twelve bustard population trends (i.e., three population trends for each zone and other three for the whole population). In addition, to test whether the population trends of each zone in the after construction phase (n=6 years) differed from random population trends we tested the significance of the slope by resampling the regression of log-abundances on year. The slopes of the regressions with the original data were compared to a resampling distribution of slopes (resampling log-abundances 999 times within the zone). We did not use this method further in the other phases because of low sample size (‘before’: n=4 years; ‘during’: n=2 years).

BDACI analysis of family groups

Annual productivity values are highly variable in this species (Palacín, 2007), so we preferred to work with density of family groups, i.e., number of family groups (mother and 1-3 chicks) present in late summer divided by the surface of each zone as a surrogate variable, and test the differences in density of family groups between phases and zones.

Results

Distance effect of the highway

The distribution of great bustard flocks among the four 500 m bands considered changed significantly during the three phases: before, during and after the highway construction (χ^2 = 21.17, d.f. = 6, P = 0.002). The main effect observed was a marked decrease in the use of the band nearest to the road (0-500 m) (53.4% during the construction phase and 56.9% after construction, with respect to the use before construction). Simultaneously, the number of flocks increased in the second band (500-1000 m) (respectively by 34.3% during and 54.6% after the construction). The changes in use of the third and fourth bands (1000-1500 m and 1500-2000 m) were less important, and combining both, the relative occupancy by flocks remained quite stable through the three construction phases (50-60%; see Appendices, Fig. A). We also found seasonal variability in the spatial distribution of flocks, although their distribution among bands did not statistically differ between the three phases in winter (χ^2 = 11.34, d.f. = 6 , P = 0.078) and late summer (χ^2 = 12.36, d.f. = 6, P = 0.054), when the occupancy declined in the first band (respectively, 69.17% and 59.3%), neither in spring (χ^2 = 4.29, d.f. = 6, P = 0.637) and early summer (χ^2 = 5.89, d.f. = 6, P = 0.436), when the occupancy of band nearest to road was quite similar (respectively, from 15.18 to 11.32% and from 10.6% to 9.71%). Regarding family groups, differences among bands were significant (χ^2 = 24.31, d.f. = 6, P < 0.001), with very marked decreases in the use of the band closest to the highway during (73.1%) and after the road construction (68.4%; see Appendices, Fig. A).

In agreement with band use analyses, most GAM models relating flock presence/pseudo-absence to distance to the highway for the phases during and after construction were significant or marginally significant (Table 1). In contrast, no model for the before construction phase was significant, and the distance to the highway explained only 0.5-5.5% of the deviance (Table 1). The shapes of the values fitted from the models show that the spatial distribution changed markedly in all cases once the construction of the highway started (Fig. 2), with the exception of spring, when changes during and after

Table 1. Deviance table of GAMs (binomial error structure) for road distance from whole year, seasonal and family group data. The models related the presence/pseudo-absence of great bustard locations with distance to the highway.

Models	Phase	Deviance explained (%)	N	χ^2	*P*
Whole year					
	Before	0.8	661	4.9	0.154
	During	9.6	288	27.1	0.000**
	After	7.7	805	57.0	0.000**
Seasonal					
Winter	Before	2.8	83	2.2	0.392
	During	22.5	40	8.2	0.043*
	After	12.7	130	13.8	0.016*
Spring	Before	1.3	217	2.7	0.329
	During	5.6	76	4.4	0.116
	After	4.7	207	10.3	0.024*
July	Before	5.5	128	7.0	0.080
	During	15.0	61	7.8	0.051
	After	7.3	189	14.8	0.003**
September	Before	0.5	233	0.8	0.637
	During	13.0	111	11.7	0.061
	After	8.3	279	22.0	0.002**
Family groups					
	Before	1.7	101	2.3	0.236
	During	24.0	44	9.3	0.030*
	After	9.2	111	9.4	0.074

Significance codes: $P > 0.5$; $*P < 0.05$; $**P < 0.01$.

construction were less pronounced. In general, the probability of presence was lower near the highway and increased progressively until reaching a certain threshold distance.

The classification trees allowed us to quantify the response threshold distances. We constructed 18 trees, of which 13 were significant and indicated the existence of threshold distances to highway (there were no significant threshold distances before the construction, except in spring and early summer). The trees that represented a year-long period identified a threshold distance of 637 m (TCC = 70%, NPP = 74%) during the construction, and two threshold distances of 259 m (TCC = 65%, NPP = 94%) and 627 m (NPP = 56%) respectively, after construction (see Appendices, Fig. B.1).

GAM and tree models showed differences among seasons (Fig. 2). In winter, threshold distances were at 752 m (during phase: TCC = 73%, NPP = 64%) and at 563 m (after phase: TCC = 68%, NPP = 80%), and the GAM

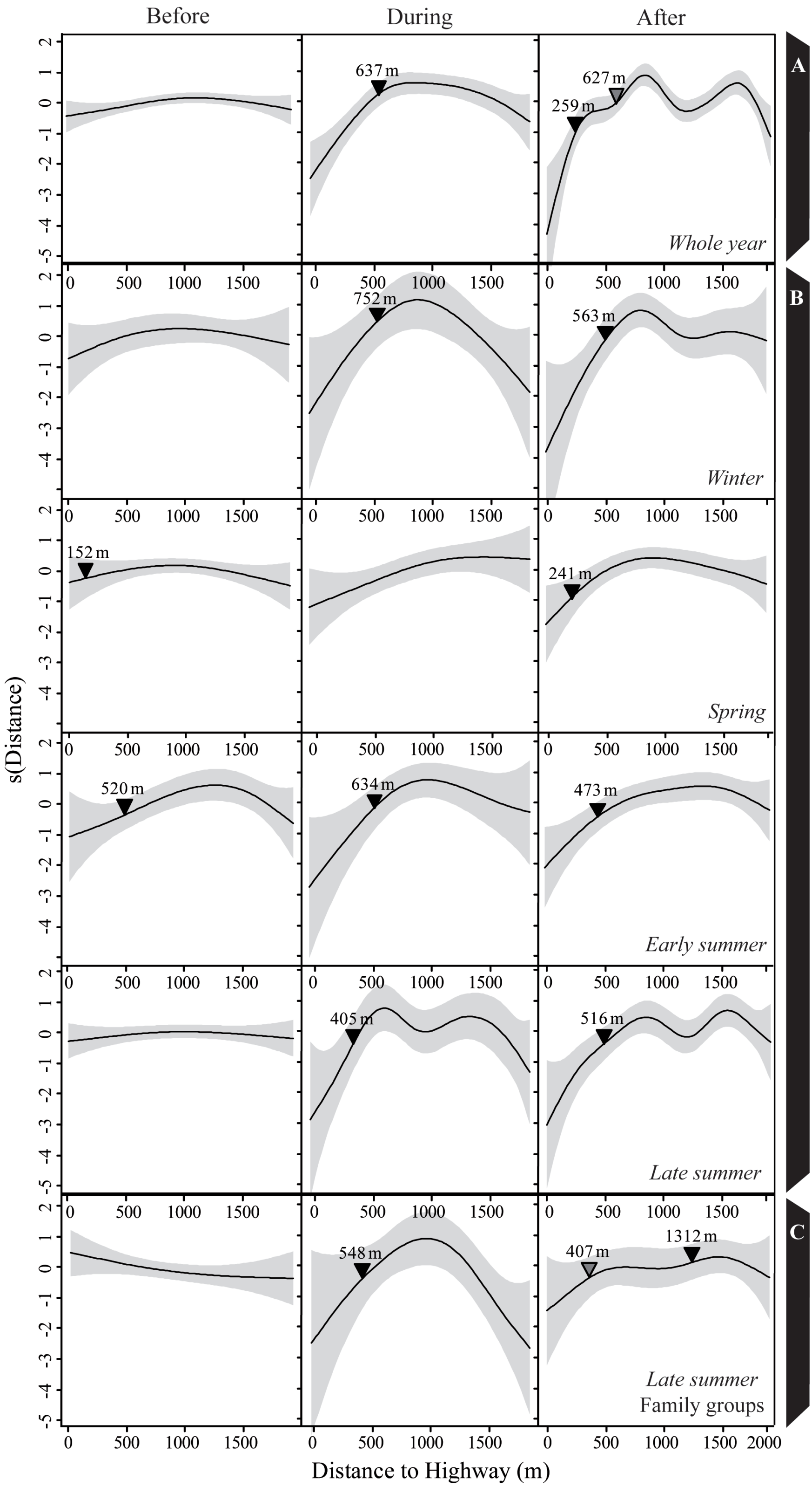
Before
During
After
A
B
C
637 m
627 m
259 m
Whole year
752 m
563 m
Winter
152 m
241 m
Spring
520 m
634 m
473 m
Early summer
405 m
516 m
Late summer
548 m
407 m
1312 m
Late summer
Family groups
s(Distance)
Distance to Highway (m)

Figure 2. Estimate response curves from predictive models and 95% confidence intervals of distance to highway (shading) on probability of presence, for the three periods considered: before, during and after the highway construction. The effects are in logit scale and standardized to mean equal to zero. The triangles mark the threshold distances selected by classification trees (main splittings = black triangles, secondary splittings = grey triangles). "A" row shows the models for whole year data, "B" for seasonal data and "C" for family groups.

models for these two phases accounted for 22.5% and 12.7%, respectively, of the original deviance (Table 1). Early and late summer tree models were quite similar, showing threshold distances at 634 m (TCC = 75%, NPP = 82%) and 405 m (TCC = 64%, NPP = 88%) during construction, and 473 m (TCC = 64%, NPP = 78%) and 516 m (TCC = 60%, NPP = 75%) after construction, with a somewhat smaller percent of deviance explained (Table 1). Spring models were the least explanatory ones, with threshold distances around 200 m both before (TCC = 59%, NPP = 62%) and after construction (TCC = 58%, NPP = 100%). Finally, the tree models built with family groups showed the greatest differences between construction and operation phases. During the construction the GAM model accounted for 24% of the original deviance, with a threshold distance of 548 m (TCC = 63%, NPP = 75%; see Appendices, Fig. B.2). However, after construction the main threshold distance reached 1312 m (TCC = 71%, NPP = 61%), with a secondary threshold at 407 m (NPP = 82%).

BDACI analysis of population dynamics

The TRIM model indicated that a significant slope change in population size occurred in 2003 (Wald test = 11.42, d.f. = 3, P = 0.009), i.e., when the construction phase finished. Change points in 1998 and 2001 were not significant (respectively, Wald test = 2.09, d.f. = 3, P = 0.553, and Wald test = 6.93, d.f. = 3, P = 0.074). Indeed, the population indices calculated by TRIM showed that population trends before and during construction were quite similar among the three zones (Table 2 and Fig. 3). During construction bird numbers increased significantly in all zones, i.e., the whole population was growing. In contrast, once the highway was built populations trends differed significantly among zones (Wald test = 33.88, d.f. = 3, P < 0.001): great bustards declined significantly in the IZ (from 363 to 211 individuals; Fig. 3), remained stable in CZ1 (mean [SD] = 220 [34] individuals), and increased significantly in CZ2 (from 411 to 567 individuals). Consequently, the overall population trend for the last phase was not significant but relatively stable with a slight trend to decrease (from 971 to 924 individuals; mean [SD] = 956 [49] individuals).In the impact zone the regression between log-abundance and year during the ‘after’ phase was significant (estimated by resampling) and showed a decreasing trend (Table 2). Year 2008 is an outlier (Bonferroni-adjusted t-test: P = 0.023), and year 2009 could be regarded as an influential point (Cook’s Distance = 0.98, almost reaching 1, which is the common threshold at which to consider a point as influential in regression, Fox, 2008). However, the slope remains negative and significant even when removing either of the years (without 2008: slope = -0.07, d.f. = 3, P = 0.001, R^2 = 97.8%; without 2009: slope = -0.11, d.f. = 3, P = 0.022, R^2 = 86.5%). By contrast, the slope of year for the ‘after’ phase in CZ2 was

Table 2. Annual population changes (in percentage) of great bustard in three zones (and the whole population) and three phases of highway construction, estimated by TRIM models of population trends and by resampling the regression of log-abundances on year. The last analysis was not applied for other phases because of low sample size (‘before’: n = 4 years; ‘during’: n = 2 years).

	TRIM results			**Resampling results**		
	% annual population change	95% IC		% annual population change	*P*	R^2
Before (1998-2001)						
IZ [a]	-2.67	-8.81	3.47	-	-	-
CZ1 [b]	-6.86	-15.9	2.18	-	-	-
CZ2 [c]	-8.99*	-17.07	-0.91	-	-	-
Whole	-3.61	-8.8	6.77	-	-	-
During (2002-2003)						
IZ	17.6*	8.73	26.47	-	-	-
CZ1	16.99*	5.65	28.33	-	-	-
CZ2	10.67*	1.33	20.01	-	-	-
Whole	15.32*	7.46	23.18	-	-	-
After (2004-2009)						
IZ	-8.54*	-10.93	-6.15	-9.18	0.008**	0.73
CZ1	-4.01	-8.04	0.01	-1.79	0.150	0.14
CZ2	11.54*	7.79	15.29	6.41	0.017*	0.68
Whole	-0.01	-2.95	1.57	-3.45	0.298	0.04

[a] IZ, impact zone.
[b] CZ1, control zone 1.
[c] CZ2, control zone 2.
Significance codes: *P > 0.5; *P < 0.05; **P < 0.01.*

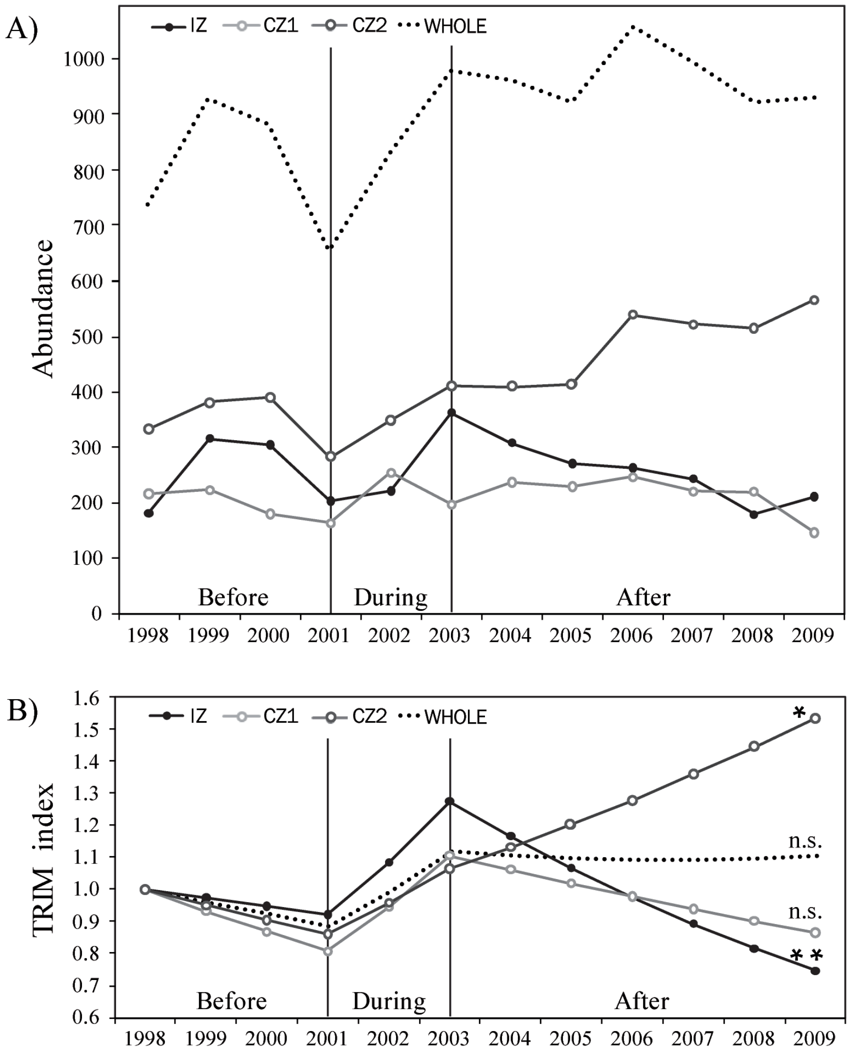

Figure 3. (A) Temporal variation of the great bustard abundance. (B) TRIM model-predicted population indexes (the "1" in the y-axis stands for the initial population sizes at the three zones) for each zone (IZ = impact zone, CZ1 = control zone 1, CZ2 = control zone 2; WHOLE = Whole Population). Vertical bars denote the three phases: 'before' (1998-2001), 'during' (2002-2003) and 'after' (2004-2009) construction of the road. The significance of the slope of each zone in the 'after' phase is shown by resampling the regression of log-abundances on year: Significance codes: n.s. (P > 0.5); *(P < 0.05); **(P < 0.01).

significant and positive (estimated by resampling), and the slope in CZ1 was not significant. Year 2009 was also an outlier (Bonferroni-adjusted t-test: P = 0.052) and was a highly influential point (Cook's Distance = 2.04). Hence, we decided to remove this observation because it had a high weight in the slope of the population trend (with 2009: slope = -0.08, d.f. = 4, P = 0.09, R^2 = 43.5%; without 2009: slope = -0.02, d.f. = 3, P = 0.288, R^2 = 14.2%). In brief, the trend for the whole great bustard population during 'after' phase was not significant (slope = -3.45, d.f. = 16, P = 0.298, R^2 = 3.9%).

Concerning productivity, the density of family groups varied widely during the study period (IZ, CZ1 and CZ2 had mean densities of, respectively, 0.31 [SD 0.17], 0.51 [SD 0.18] and 0.65 [SD 0.30]), although the density recorded in the IZ was smaller than in both control zones. However, the trends were similar among zones, with years of marked growth and years of steep falls. The density did not differ significantly among construction phases (ANOVA, F = 0.02, P = 0.982) and changes were concomitant among zones (the phase-zone interaction was not significant either F = 0.48, P = 0.752).

Discussion

Our study exemplifies the conflict between conservation goals and the growth of road networks. The results showed that great bustard use of areas near a highway decreased during and after road construction, implying a significant loss of habitat for this species. Demonstrating road effects on wildlife has been challenging, due to methodological limitations or study design flaws (Balkenhol and Waits, 2009; Benítez-López et al., 2010). BACI designs are strongly recommended as the most powerful tools to avoid most of these flaws and to clearly identify the effects of human infrastructures (Roedenbeck et al., 2007; Stewart-Oaten and Bence, 2001). To our knowledge, this is one of the first studies using BDA and BDACI designs to determine the effects of the construction of a highway on an animal population. All studies about road effects, including those using BACI, are biased to some extent, because the impact zone is nonreplicable (Stewart-Oaten and Bence, 2001; Underwood, 1992), and roads are not randomly distributed across the landscape because their location is planned according to topographic and others suitability criteria (Stewart-Oaten and Bence, 2001). This means that it will be difficult to extrapolate conclusions from non-randomly selected sites. In spite of this difficulty, the BACI approach is still recommended when a time series including data before the intervention is available for both the impact zone and control zones (Roedenbeck et al., 2007; Stewart-Oaten and Bence, 2001). Some authors have suggested caution when interpreting results, particularly when few species change their behaviour or the responses detected are not strong, because in such cases it would be difficult to discard the effects of alternative potential causal factors (Schroeter et al., 1993). In our study, however, we could clearly identify and measure the avoidance behaviour of great bustards, and detect a marked change in the species' population trend in the impact zone.

Distance effect from highway and seasonal patterns of threshold distances

The combination of GAM and tree models has proven to be a useful framework for obtaining a realistic representation of the species' response to the road construction. This approach could likely be applied to all linear infrastructures with others species. Furthermore, as opposed to analysis by bands, this procedure avoids the problems derived from a subjective delimitation of bands. Although explained deviance may seem low, the models are univariate. Also, values adjusted by the model suggest that distance to road has a considerable effect up to a certain distance, while farther away from the road other variables have an effect on the presence/absence of flocks. In other words, distance is an important explanatory variable for a limited sector of the 2 km band, which reduces the total variance explained. Indeed, the predictive capacity of threshold distances obtained from classification trees was much higher (NPP averaged roughly 80%). Overall, the threshold distances in the models averaged ca. 630 m from the highway, with a minimum occupancy within 259 m. The greatest changes in the spatial distribution happened within the 1000 m band nearest to the road, with a possible local movement from the 0-500 m to the 500-1000 m band.

Several studies have shown that animals respond in different ways to different types of human activities, depending on certain characteristics like speed, noise, or the potential danger these activities imply (Riddington et al., 1996; Sastre et al., 2009). In our case, the distance effect became apparent during the construction, and later also during the operation phase, which suggests that both building activities and car traffic caused avoidance behaviour in the great bustard.

The response of great bustards was not the same in all phases of their annual cycle. Threshold distances were highest during winter, whereas GAM and tree models obtained in spring were not sufficiently explanatory to suggest a considerable effect during this season. These results agree with a previous habitat selection study showing that winter locations are less fixed than lek sites in this species, and located at greater distances from the nearest roads (Palacín, 2007). A plausible explanation is that in spring, the distribution of great bustards is strongly conditioned by the need to aggregate at traditional lek sites (Alonso et al., 2000). Strong site fidelity has also been reported for most lekking species (Höglund and Alatalo, 1995). Great bustards showed a clearly avoidance behaviour in summer as well. Particularly family groups were less tolerant, as shown by their higher distance effect as compared to flocks, with a low occupancy up to 1300 m. Mothers probably prioritized minimizing risks for their offspring, and thus selected territories far from road disturbances.

Some studies with other species also reported that responses to road disturbances may change throughout the year. For example, seasonal patterns have been described for roadkills and related to seasonal changes in habitat preferences or dispersal movements (Grilo et al., 2009; Smith-Patten and Patten, 2008). Traffic-volume and noise have often been considered the most decisive factors causing changes in bird distribution patterns near roads (Forman et al., 2002; Reijnen and Foppen, 2006). Our study area was quite noisy long before the road construction began, due to the presence of a nearby airport, so the avoidance behaviour could be more related to the construction works and traffic volume. However, the absence of substantial seasonal fluctuations in traffic volume (mean [SD] = 7437 [3152] vehicles/day in winter, 9009 [3724] vehicles/day in spring, 10 116 [3218] vehicles/day in early summer and 9321 [3100] vehicles/day in late summer; data from the highway company HENARSA), suggests that the temporal pattern in bird distribution could depend on other behavioural features of the species.

Changes in population dynamics

The analyses of population trends and productivity combining TRIM and BDACI allowed us to ascertain any changes in population size, a crucial issue for conservationists (Gill et al., 2001; Sutherland, 1996). Population trends observed prior to and during road construction were rather similar in the impact zone and both control zones, and they also coincided with overall trends in a much wider region (Martín, 2008). In contrast, after the highway construction there was little agreement in the population trends between impact and control zones. During the construction the whole population was growing and suddenly in 2003 (when the highway was fully operative) the trends changed: the population gradually declined in the impact zone, while it remained stable in the closest control zone and increased in the farthest. This suggests that a new process would be affecting population dynamic. Neither a potential decrease in productivity in the impact zone, which was smaller than in both control zones through the whole study period, nor roadkills, which have never been reported in our study area, seemed to contribute to that population decline. A more plausible explanation, which is supported by the general stability of the whole great bustard population in our study area and in a wider region (Martín, 2008; unpublished data), is that a number of birds could have moved from the impact zone to the farthest control zone as a consequence of the road construction. Studies based on extensive radio-tracking of marked individuals (Alonso et al., 2004; Martín et al., 2008) have shown that the settlement of dispersers is highly determined by the presence of conspecifics (i.e., through conspecific attraction, see Danchin and Wagner, 1997), thus we suggest that the lower disturbance levels and the higher number of conspecifics in the farthest control zone were decisive in the population changes observed.

Methodological aspects

The methodological framework including a long-term series of surveys and BDA and BDACI designs has allowed us to detect and quantitatively assess the effects of the road construction with high inferential strength. In addition, the selection of two control zones at different distances from the highway was useful to identify and confirm some road effects and to understand the bird responses at the scale of the whole population. We strongly recommend using such a variable range of spatial scales in future impact studies.

BDACI design can be applied in Road Ecology to assess both road effects and effectiveness of mitigation measures. However, ecological impact assessments are usually conducted under time constraints that make the collection of previous data and application of BDACI design difficult. Unfortunately, feasibility of the studies declines with the inferential strength, because of the greater number of design requirements that must be fulfilled and the number of resources required to fulfill them (Roedenbeck et al., 2007). BDA design would appear to work well only for assessing population changes for temporally invariant taxa (i.e., those in steady-state equilibrium; Wiens and Parker, 1995), because the assessor would expect the population trends to be equal in the absence of highway, assuming that natural variation is similar between before, during and after sampling phases. Regarding CI design, the difference between impact and control zones is valid only if control and impact zones are identical in the absence of highway, an assumption that cannot be tested, because the before-after component is missing (Osenberg and Schmitt, 1996). If our study had started when the road was opened to traffic it would have detected a population decrease in the impact zone. However, it would not be clear whether such decrease was a consequence of previous population trends, which in such a study would be unknown. In the end, the research question addressed and the study species (temporal dynamic, recovering rates, spatial distribution, etc.) will determine the particular study design selected and the length of monitoring program (see a hierarchy of study designs in Roedenbeck et al., 2007).

Conclusions and management implications

The current and future trends of agro-steppe landscapes may be explained by three change vectors: urbanization, agricultural intensification and land abandonment (Santos and Suárez, 2005). Southern European countries still hold well-preserved agro-steppe areas, but the increasing construction of infrastructures (e.g., highways, railroads or power lines; e.g., Martínez-Abraín et al., 2009) and urban sprawl are one of the highest threats of habitat fragmentation, which may imply serious risks for endangered species living in these areas. Regarding protected areas, this study highlights the conflicts between conservation efforts and expansion of the infrastructures. Hence, there is an increased need for management proposals to enforce the policy concerning the Natura 2000 network. Member states of European Union have to take appropriate steps to avoid deterioration of habitat or any disturbances affecting birds (Directive 2009/147/EC), so they must pay more attention to new linear infrastructures.

In the present work, although the effects of the highway did not necessarily imply a decrease in the overall population size, they caused changes in the space use patterns of species, and ultimately contributed to a higher aggregation, which might in turn lead to a loss of genetic diversity, as well as a higher vulnerability due to demographic and environmental stochasticity (Epps et al., 2005). Our results contributed to increasing the knowledge about the functional responses of great bustards to roads, and to quantifying some of the negative effects of these infrastructures, thus they should be considered when planning and evaluating alternative road alignments.

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Appendices

Figure A. Histograms for the relative frequency of great bustard flocks for each phase of the highway construction.
Figure B. Classification tree describing the pattern of distances to the highway of the year-round locations during the road construction (Fig. B.1) and during the operation phase (Fig. B.2).

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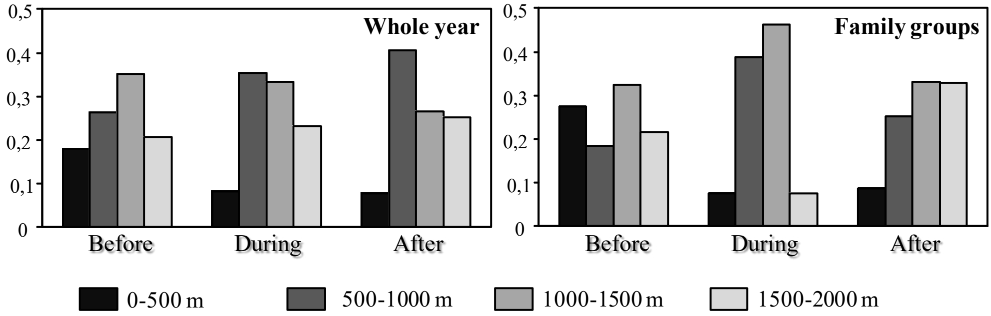
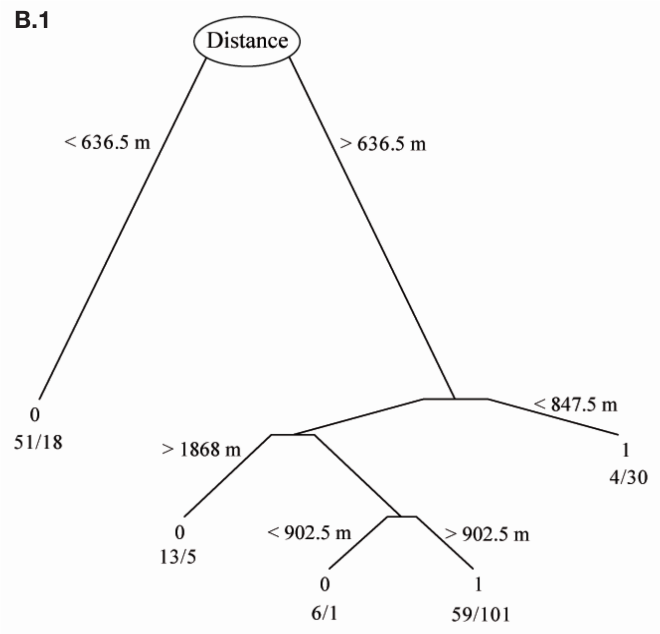


Figure A. Histograms for the relative frequency of great bustard flocks for each phase of the highway construction.

B.1



B.2

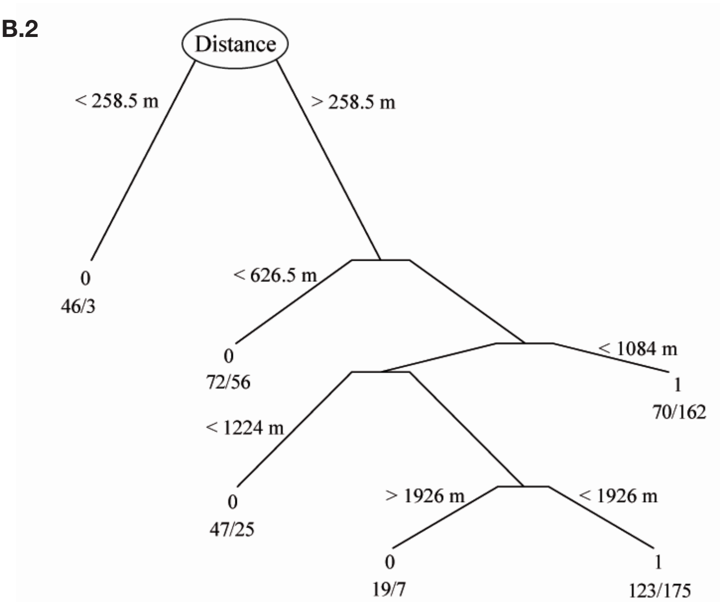
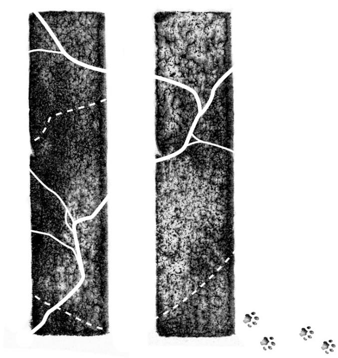


Figure B. Classification tree describing the pattern of distances to highway of the whole year locations of great bustard' flocks during the road construction (Fig. B.1) and during the operation phase (Fig. B.2). Branch lengths below each split are proportional to the amount of deviance explained by the classification variable at the split. The end nodes or "leaves" of the tree are labeled with the two classes of the response variable: 0, pseudo-absence; 1, presence. Numbers below the end node labels refer to the number of flocks classified into that node; the first number indicates the number of pseudo-absences placed into that leaf, and the second indicates the number of presences in the leaf.

Chapter

Capítulo



Respuestas de la fauna a estructuras humanas a gran escala: Un enfoque novedoso para evaluar el impacto del desarrollo de infraestructuras

Resumen

Las carreteras y los asentamientos humanos contribuyen al declive y a la extinción de las especies de fauna silvestre, pero normalmente se pasan por alto los efectos a gran escala de estas estructuras. En este estudio analizamos la red europea de infraestructuras de transporte y encontramos que el 50% del continente está a menos de 1.5 km de la infraestructura más cercana. A continuación, presentamos un método novedoso para evaluar los impactos de infraestructuras en la fauna salvaje, basados en curvas de respuesta funcional que describen reducciones en la densidad de aves y mamíferos con la distancia (e.g., zonas de efecto de carreteras), y lo aplicamos a España como caso de estudio. La huella de las infraestructuras se extiende sobre la mayor parte del territorio (55.5% en el caso de las aves y 97.9% en el caso de los mamíferos), prediciendo un declive moderado en aves (22.6% de los individuos) y declives severos en mamíferos (46.6%). A pesar de ciertas limitaciones, sugerimos que la aproximación es ampliamente aplicable para evaluar los efectos de los desarrollos urbanísticos en fase de planificación bajo múltiples escenarios y proponemos una estrategia coordinada internacionalmente para actualizarla y mejorarla en el futuro.

Torres, A., Jaeger, J.A.G., Alonso, J.C. Large-scale wildlife responses to human structures: A novel approach to assessing the impact of infrastructural development. Under review in Conservation Letters.

Large-scale wildlife responses to human structures: A novel approach to assessing the impact of infrastructural development

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Abstract

Roads and human settlements contribute to the decline and extinction of wildlife species, but large-scale effects of these structures remain generally overlooked. We analyzed the European transportation infrastructure network and found that 50% of the continent is within 1.5 km of a transportation infrastructure. We present a novel method for assessing the impacts from infrastructure on wildlife, based on functional response curves describing density reductions in birds and mammals (e.g., road-effect zones), and apply it to Spain as a case study. Infrastructure imprint extends over most of the country (55.5% in the case of birds, and 97.9% in mammals), predicting moderate declines in birds (22.6% of individuals) and severe declines in mammals (46.6%). In spite of certain limitations, we suggest the approach proposed is widely applicable to evaluate effects of planned infrastructure developments under multiple scenarios, and propose an internationally coordinated strategy to update and improve it in the future.

KEYWORDS Anthropogenic development, birds, Europe, habitats, mammals, road-effect zone.

Introduction

Habitat loss and degradation are the primary drivers of the decline and extinction of wildlife populations in terrestrial ecosystems (WWF 2014), and their main precursors are roads and human settlements (Forman et al. 2003). If current trends continue, by 2030 urban areas will increase by 1.2 million km^2, and our planet will accommodate more paved-lane kilometers than those required to reach Mars by 2050 (Seto et al. 2012; Dulac 2013). These structures alters ecological conditions and reduces populations of many species (Fahrig

& Rytwinski 2009; Clarke et al. 2013). However, large-scale consequences of these trends remain unknown (van der Ree et al. 2011).

Human footprint models combine spatial data about several threats with assessments of their impacts to estimate footprint (Sanderson et al. 2002; Woolmer et al. 2008; Theobald et al. 2012). The burgeoning availability of detailed geospatial layers of infrastructure contrasts with the lack of quantification of their effects, which still rely on expert knowledge and are mostly based on single species or local studies (e.g., Forman & Deblinger 2000). As a result, mapping of its area of influence ranges from a few hundred meters (González-Abraham et al. 2015) up to 30 km (Sanderson et al. 2002; Carver et al. 2012; Selva et al. 2015).

The main difficulty in quantifying the area of influence of infrastructure on wildlife (e.g., 'road-effect zone'; Forman et al. 2003) has been the lack of reliable distance thresholds for these effects (Leu et al. 2008). Most effects on local species abundances occur within a specific distance from the infrastructure and level off as distance increases (Palomino & Carrascal 2007; Eigenbrod et al. 2009). For instance, this descent in population density varies by taxonomic class, with mammals being affected over larger distances than birds (Benítez-López et al. 2010).

Our objective is to present a novel method for assessing the spatial extent of the impacts from infrastructure on wildlife populations at large scale, based on taxa-specific functional distance-decay curves. We first examine the pervasiveness of European transportation infrastructure and then, highlighting Spain as an example, explore the effects of infrastructure on the distribution of six emblematic species of the Iberian fauna, and apply our approach to model the area of influence of infrastructure for birds and mammals. The Mediterranean Basin is the biodiversity hotspot most affected by urban expansion worldwide (Seto et al. 2012), and thus results for Spain may help predicting the level of threat of other biodiversity hotspots undergoing rapid development.

We revealed both the pervasiveness of human infrastructure and its potential to negatively influence wildlife populations, particularly among wide-ranging mammals. Despite its limitations, our approach may represent a useful tool for conservation and land management, enabling: (i) assessments of the human footprint of infrastructure or wilderness mapping, (ii) the definition of roadless areas, and (iii) projections of future human influence under alternative scenarios.

Methods

Distance analysis

We measured proximity to transportation infrastructure in inland Europe (and islands larger than 3,000 km^2 as well as Malta) based on EuroGlobalMap v7.0 (EGM; 1:1,000,000 scale; EuroGeographics, 2014). We considered exclusively paved roads and railway lines, excluding abandoned and underground sections (Table S1). Then, we calculated Euclidean distances to the nearest transport infrastructure for 39 countries, at a resolution of 50 m.

Consistency of EGM database was assessed against the most recent and precise GIS database of transportation infrastructure for Spain (BCN100, 1:100,000 scale; IGN, 2014; Table S2). In addition, we measured the pervasiveness of built-up areas and all infrastructure combined. We used the Spanish land cover and use information system (SIOSE, 1:25,000 scale; IGN 2005) to create the map of built-up areas (Table S3) and other impervious infrastructure (e.g., parking lots, irrigation ponds; Table S3). All maps were converted to raster format (15 m). For each cell, we calculated the Euclidean distance to the nearest transport infrastructure, built-up area, and all impervious infrastructure combined.

Effects of proximity to transportation infrastructure on species distribution

We overlaid distance maps to transportation infrastructure with distribution maps of six emblematic species of the Iberian fauna known to be negatively affected by roads at local scales; *Strix aluco* (Tawny owl), *Otis tarda* (Great bustard), *Aquila adalberti* (Spanish imperial eagle), *Canis lupus* (Grey wolf), *Lynx pardinus* (Iberian lynx), *Ursus arctos* (Brown bear) (10x10 km cells; MAGRAMA 2012). For each species, we quantified the medium distance to transport infrastructure in presence cells and classified resulting distances by bands of 500 m from the nearest infrastructure for graphical representation as a normalized histogram. Counting how many presence cells fell into each 500 m band, we calculated both the relative proportion of the species distribution that each band represented and their prevalence, i.e., the presence cells divided by the total of cells in each band.

Modeling the area of influence of infrastructure

We estimated the overall effect of the Spanish transportation, and other impervious infrastructure on mean species abundances for birds (MSA_b) and mammals (MSA_m) and determined the spatial distribution of the predicted effect zone. The *MSA* indicator expresses the difference between the averaged mean abundance for various species in the proximity of an infrastructure relative to their abundance in a control location free of infrastructures (Alkemade et al. 2009). *MSA* values range from no individuals remaining (0) to no effect on species abundance (1). Using a meta-analytical approach, Benítez-López et al. (2010) tested the relationship between *MSA* and distance to infrastructure through GLMM, and provided functional distance-decay curves of response for birds and mammals (Figure 1). This study was undertaken using 49 studies and 90 datasets, which included 201 bird (52% present in Spain) and 33 mammal species (12% present in Spain), but shows a substantial geographic bias since 88% of the studies came from Europe and North America.

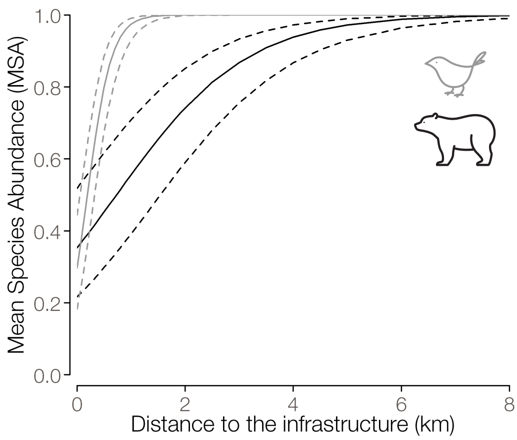

Figure 1. Relationships between mean species abundance of birds and mammals and distance to infrastructure obtained by Benítez-López et al. (2010) through meta-regressions and used in this study to model the area of influence of infrastructure in Spain. Solid lines represent the estimated curve of the decline of *MSA* of birds (gray) and mammals (black), related to distance. Dashed lines represent the 95% confidence bands for the predictions.

Based on the statistics from the meta-analysis, we generated two spatial datasets on the predicted infrastructure effects on birds and mammals and four spatial datasets showing the associated upper and lower 95% Confidence Intervals (CI) at a resolution of 15 m by applying a logit transformation:

$$MSA_{(\text{estimated})} = \frac{e^u}{1 + e^u},$$

where *MSA*(estimated) is the predicted *MSA* at the observed distance from the infrastructure and *u* is the linear equation describing the log-transformed probability of the presence of a species at a certain distance *x* from the infrastructure:

$$u = \ln\left(\frac{P_i}{1 - P_i}\right) = \beta_0 + \beta_1 x,$$

where β_0 is the intercept (β_0-birds = -0.863; β_0-mammals = -0.607) and β_1 is the regression coefficient for the distance (β_1-birds = 0.00447; β_1-mammals = 0.00083). The coefficients where obtained from the authors of the meta-analysis. The distance variable *x* could take the value of each cell in raster containing the Euclidean distance from an infrastructure. Given that 61.1% of the datasets considered by Benítez-López et al. (2010) corresponded to roads-effects and the rest to other infrastructure, we used both a raster of distances to transportation infrastructure alone (as a conservative measure), and another with all impervious infrastructure combined to explore the sensitivity of our estimates.

Finally, we analyzed the overall effect of the infrastructure by habitat types on a national scale, by overlaying distance and *MSA* layers on a land cover map (Corine-2006; http://www.eea.europa.eu/data-and-maps/data/clc-2006-vector-data-version-3) and calculating statistics for each habitat. We report the results for five major classes in the main text – namely, wetland, bare land (open space with little or no vegetation), farmland, scrubland, and forest – but the results for classes at finer thematic resolution are available in Table S5.

Results

How far to the nearest infrastructure?

Twenty percent of all land area in Europe is located within 430 m of the nearest transport infrastructure, and 50% is within 1.5 km (Table S4). These distances are only slightly reduced for the EU-28 (424 m and 1.5 km respectively). 95% of all Europe and EU-28 was located within 9.2 km and 8 km of a transport infrastructure respectively, with farthest distances in Iceland (83.5 km). Central Europe, and particularly Benelux countries, concentrates the

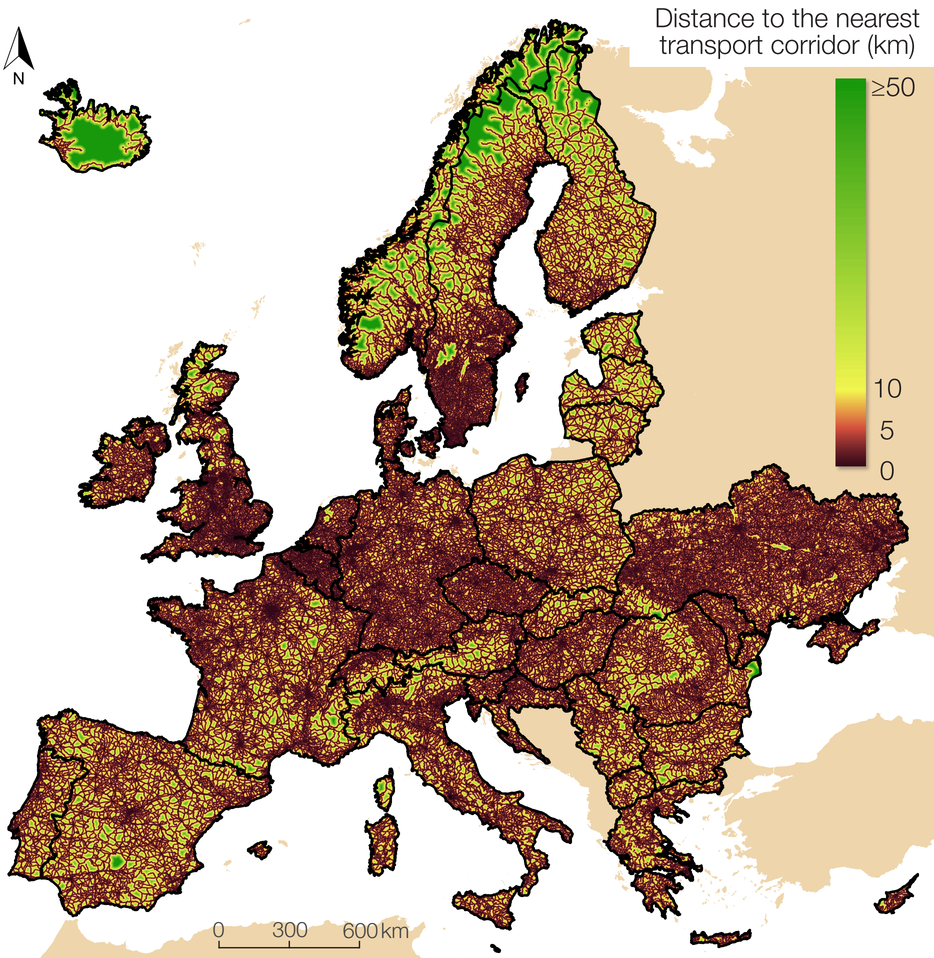

Figure 2. Mapped distances to the nearest transport infrastructure (paved roads and railways; details in Table S1) based on the small scale pan-European topographic dataset EuroGlobalMap v7.0 (2013). Distances were quantified at a resolution of 50 m for inland Europe and islands larger than 3,000 km^2 and ranged from 0 to 83.5 km. Shown using a Lambert Azimuthal Equal Area projection.

densest transport network (Figure 2), whereas low density patches are accumulated in northern latitudes and big mountain ranges (Alps, Carpathians). Spain stands out as the country with the highest medium and average distances to transport infrastructure (1.9 and 2.7 km respectively), excluding Iceland, Fennoscandia, and Andorra. This median distance is almost halved based on the more precise BCN100 (869 m), revealing the underrepresentation of transport infrastructure in the EGM. Besides transportation infrastructure, 50% of all land area in Spain is located within 1.6 km the nearest built-up

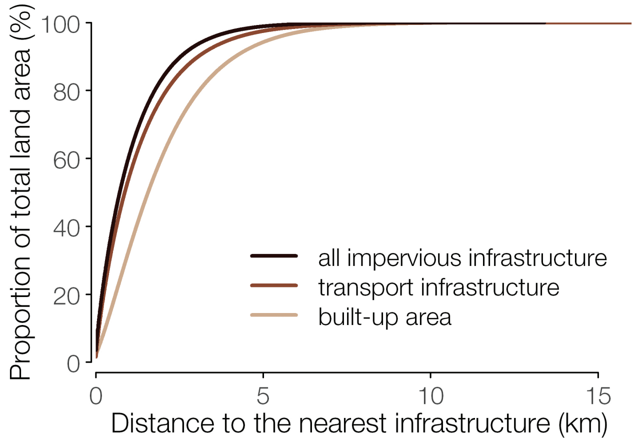

Figure 3. Accumulation curves for the proportion of total land area located within a certain distance from the nearest built-up area, transport infrastructure (paved roads and railways), and impervious infrastructure (including built-up areas, transport infrastructure, and other sealed surfaces) in Spain.

area and 718 m from the nearest impervious infrastructure (Figure 3). Most land is located near infrastructure, and the proportion of land added to the curve rapidly becomes smaller as the distance increases, so 99% of Spanish land is within 7.6, 6.4, and 5.2 km from a built-up area, transport corridor, and impervious infrastructure respectively, while the farthest locations are at 15.4, 16.6, and 13.4 km.

Regarding the effects of infrastructure proximity on emblematic species distributions, all six species are mainly found within the second 500 m band (Figure 4). However, prevalence values show differences between taxa, being higher at increasing distances to transport infrastructure in the Spanish imperial eagle, Iberian lynx, and Brown bear, and showing no clear pattern in the Tawny owl, Great bustard, and Grey wolf.

What is the area of influence of infrastructure on birds and mammals in Spain?

The area of influence of infrastructure, considering a *MSA* < 0.95 covers 55.5% (CI = 48.3-64.4%) of the country in the case of birds, and extends over almost all of Spain for mammals (97.9%, CI = 95.1-99.2%). The figures for transportation infrastructure alone are very similar (birds: 49.4%, CI = 42.6-58.0%; mammals: 95.8%, CI = 91.8-98.2%). For birds, spatial clusters of low *MSA* values are clearly observed, but large unaffected areas remain

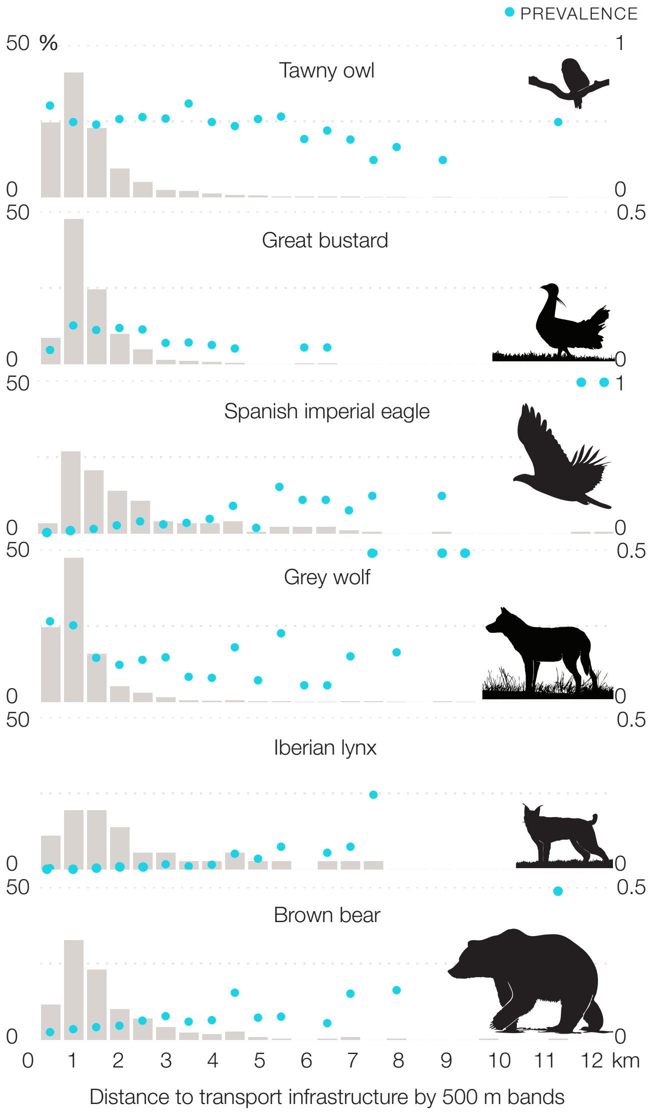

Figure 4. The level of exposure to human infrastructure varies throughout a species' distribution, which we illustrate by considering the distributions of six emblematic species of the Mediterranean fauna (c). The bars (left y-axis) indicate the proportions of each species' distribution that is found within the distance to transport infrastructure indicated in the x-axis. Distances were grouped by 500 m bands. The blue dots (right y-axis) indicate the prevalence for each band, i.e., the ratio between the number of cells in which the species was present divided by the total number of cells available at such distances in peninsular Spain.

available (Figure 5a), whereas for mammals low *MSA* values prevail across Spain (Figure 5b; Figure S1 for transport infrastructure alone). These *MSA* values predict an average decline of 22.6% (CI = 16.7-29.7%; for transport

a)
MSA birds

b)
MSA mammals

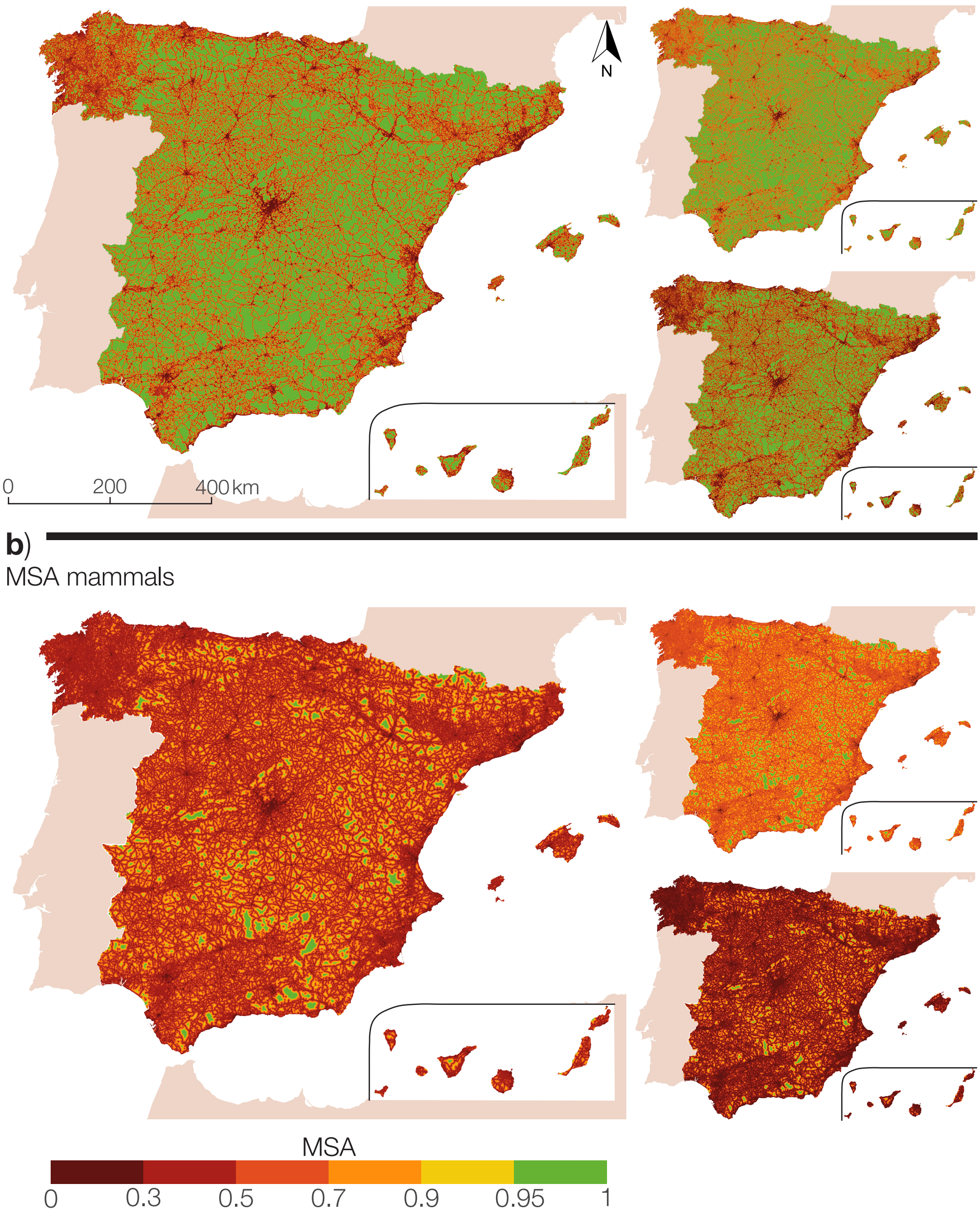

Figure 5. Predicted mean species abundance (*MSA*) of birds (a) and mammals (b) across Spain according to proximity to human infrastructure, based on the effect distance-decay curves fitted for empirical data by Benítez-López et al. (2010). The adjacent smaller maps represent the upper (up) and lower (down) confidence intervals. *MSA* layers were reclassified into 6 effect intensity zones for representation.

infrastructure alone: 19.0%, CI = 9.6-25.6%) in bird numbers, and 46.6% (CI = 33.0-60.7%; for transport infrastructure alone: 42.9%, CI = 29.6-56.9%) in mammal numbers compared to the undisturbed situation.

Are all habitats similarly affected?

Farmland is the habitat most affected by transport infrastructure and built-up areas, and where lowest *MSA* values are found (mean ± SD = 0.729 ± 0.277 and 0.496 ± 0.168, respectively for birds and mammals; Figure 6b). The second most affected habitat is wetlands (birds: mean ± SD = 0.790 ± 0.254; mammals: 0.539 ± 0.176,), due mostly to the influence of maritime wetlands (Table S3). Forests and scrublands share similar effect values, while bare lands are the least affected. In the remotest locations (beyond 10 km to impervious areas), the differences among habitats are more evident. Those locations mainly correspond to bare rocks (32.8%), natural grasslands (23.6%), and sclerophyllous vegetation (22.9%).

Discussion

In Europe, half of the continent's surface is located within 1.5 km, and almost all land within 10 km from a paved road or a railway line. Riitters & Wickham (2003) reported shorter distances to the nearest road in the US, where 50% of the land was within 382 m of a road (compared to 869 m in Spain), not only because the US road system included unpaved roads, but also probably because it was really designed to maximize access to any location in the country. Given that the more accurate input map of paved roads and railway lines halved the estimated distance from EGM, we consider the European estimates to be very conservative.

Spain is one of the European countries less affected by road-mediated effects but on the other hand, is under a high human footprint from a global perspective (Kareiva et al. 2007). All of our example species were more abundant at relatively close distances to transportation infrastructure, because most of the land is located at such distances (Figure 3), so wildlife do not have many options of occupying remote areas. Indeed, the increasing prevalence of some species with higher distances to transport infrastructure suggests that they prefer remote sites (Spanish imperial eagle, Iberian lynx, and Brown bear). These detrimental effects at large scale illustrate the high level of exposure for wide-ranging carnivores, like the critically endangered Iberian lynx,

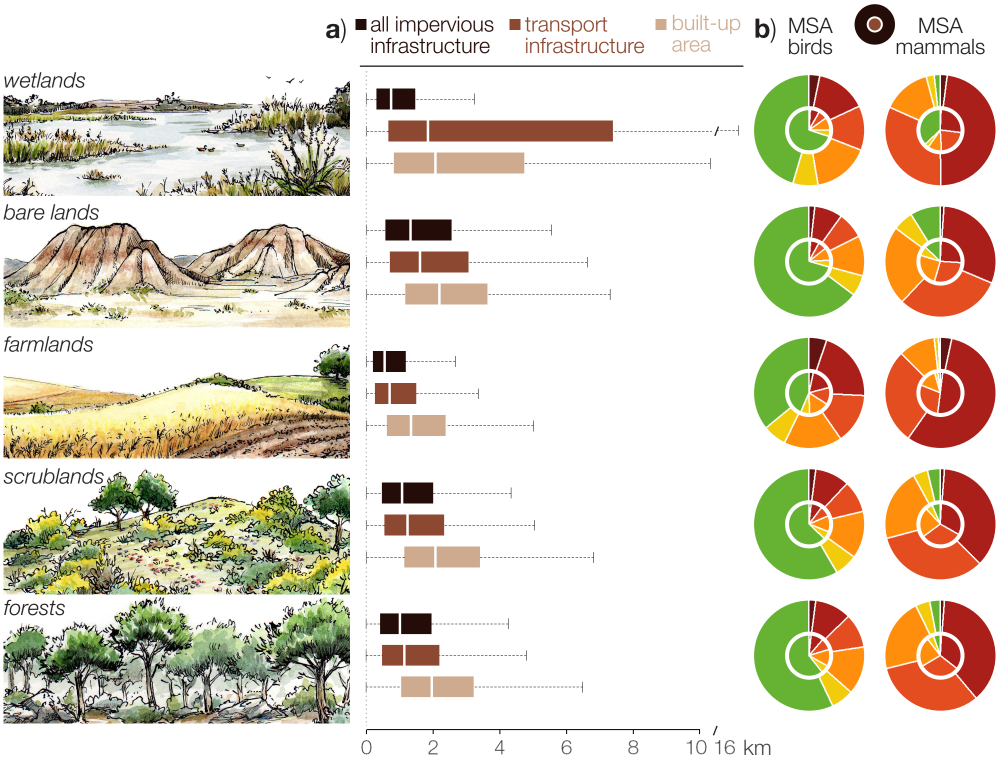

Figure 6. (a) Box plots of the distances to the nearest built-up area, transport infrastructure, and all impervious infrastructure combined, for the five habitat types considered. (b) Proportion of land that falls inside each intensity zone (see Figure 2) for birds and mammals per habitat type, based on proximity to impervious infrastructure (outside circle) or transport infrastructure alone (inside circle). Colors correspond to *MSA* legend in Figure 2. [Habitat illustration credits: Marina Pinilla]

for which road casualties are a major mortality cause (20 road-kill mortalities in 2014 in a total population of ca. 320 individuals; http://www.iberlince.eu). In contrast, the Tawny owl and the Gray wolf are known to use areas next to roads (Colino-Rabanal et al. 2011; Grilo et al. 2014), whereas the Great bustard is characteristic of cereal farmland, a habitat strongly pervaded by infrastructure (Figure 6).

Area of influence of human infrastructure for birds and mammals

Proximity to infrastructure contributes to average decreases of 25 and 50% compared to the undisturbed situation, in birds and mammals, respectively, based on data from Benítez-López et al. (2010). Moreover, in the case of mammals there is almost no area left unaffected from transport infrastructure. For Road Ecology, it implies that researchers may no longer be able to measure the whole extent of the road effects on wide-ranging mammals – and birds with large effect-distances –, since core areas of significant size that could be used as controls are now almost inexistent, and this extends to most of Europe and a sizeable part of the US (Figure 2; Watts et al. 2007).

Our analysis provides the most detailed picture obtainable nowadays of the magnitude and spatial distribution of infrastructure-induced effects on birds and mammals and contributes important information to regional or national planning. Areas characterized by a low imprint of infrastructure may clearly be priority sites when it comes to protecting roadless areas (Dickson et al. 2014; Selva et al. 2015). However, some places still hosting important biodiversity are no longer in remote areas, suggesting that extinction debts are likely. In this regard, the prevented reductions in bird and mammal numbers are inherently based on how we have managed wildlife over the past decades in the affected areas. Hence, areas with a high imprint of infrastructure have become challenges for conservation planning, where extinctions (which are currently debts) should be prevented by reinforcing remnant populations, and restoring vital ecological processes.

Applicability of the approach and next steps

This approach explained for Spain is readily transferable to other places. However, it has certain limitations: (i) geographic bias, (ii) undistinguished effects of different infrastructure types, and (iii) low inferential strength of the works considered in the meta-analysis. The geographic bias is not a major problem in our case because studies from Europe are well represented, but may limit the applicability of this approach beyond Europe and North America. As for (ii), previous studies have found different effects for different road types or traffic levels (Reijnen et al. 1996), which would affect the accuracy of estimates. However, there is still a substantial debate around this topic and thus we decided to ignore differences between infrastructure types to keep consistency with Benítez-López et al. (2010) who did not find a significant difference. Finally, most works used in the meta-analysis followed a Control-Impact study design, by comparing bird and mammal numbers in the impacted area with a reference state. Although this is a widely used design to quantify impacts from a variety of pressures (e.g., Chaplin-Kramer et al. 2015), it has lower inferential strength than a Before-After-Control-Impact

(BACI) design (Torres et al. 2011). Unfortunately, due to time and logistical constraints, the proportion of BACI-designed studies is still very small (Lesbarrères & Fahrig 2012).

Most of the urban development and more than one third of the transportation infrastructure expected to exist by 2050 is not yet built (Seto et al. 2012; Dulac 2013). As infrastructure building progresses it will be increasingly difficult to quantify their effects, since the areas that can be used as controls will be rare and more isolated. Therefore, there is a compromise between the uncertainty of using effect measures from studies with low inferential strength and the urgent need to respond to the rapid development using the evidence available today, subjected to the precautionary principle. We propose to overcome, at least partially, the weaknesses of our approach through regular updates of the wildlife-response meta-analysis. The addition of new species' data sets would allow fine-tuning the parameters of the response functions, and the selection of certain groups of species with similar functional traits might provide new response functions relevant for specific cases, for example when conservation needs to be focused on particular taxa or wildlife communities. In moving forward, we are making a call to scientists and practitioners to coordinate a database and network of studies about infrastructure-mediated impacts on wildlife populations across ecosystems and geographical areas (van der Ree et al. 2015), which could serve as a powerful conservation planning tool.

Acknowledgements

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Supplementary material

Table S1. Linear transport infrastructure considered, with their corresponding buffer width, in Europe.

Table S2. Linear transport infrastructure considered, with their corresponding buffer width, in Spain.
Table S3. Attribution of the land covers from the SIOSE project to map built-up areas and other impervious infrastructure.
Table S4. Summary statistics of the distances to the nearest transport infrastructure per country.
Table S5. Summary of the distances to the nearest built-up area, transport infrastructure, and all impervious infrastructure combined, by habitat type.
Figure S1. Predicted mean species abundance (*MSA*) of birds (a) and mammals (b) across Spain, according to proximity to transportation infrastructure. The adjacent smaller maps represent the upper (up) and lower (down) confidence intervals. *MSA* layers were reclassified into 6 effect intensity zones for representation.

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Supplementary material

Table S1. Linear transport infrastructure and their corresponding buffer widths considered in this study for Europe, from the small scale pan-European topographic dataset EuroGlobalMap v7.0 (1:1,000,000 scale; 2013). Underground or abandoned sections were excluded, as well as roads whose surface type was loose/unpaved. Settlements (population ≥ 50,000 inhabitants and size ≥ 0.5 km^2) were merged to this layer since transport infrastructure inside urban areas is commonly underrepresented.

Element	Buffer (m)
Motorway	15
Primary route	10
Secondary route	6
Local route	5
High-speed railway	4
Conventional railway	2

Table S2. Linear transport infrastructure and their corresponding buffer widths considered in this study for Spain, from BCN100 database (1:100,000 scale; National Geographic Institute of Spain, 2014). Underground or abandoned sections were excluded, as well as unpaved roads.

Element	Buffer (m)
Motorway (*Autopista*)	15
Motorway (*Autovía*)	15
National road	10
Autonomous road	6
Connecting road	5
Street	5
High-speed railway	4
Conventional railway	2

Table S4. Summary statistics of the distances to the nearest transport infrastructure (m) per country sorted by increasing median distance. Details of the infrastructure included and their buffer areas are available in Table S1. It should be noted that distances were quantified for inland Europe and islands larger than 3,000 km^2 (except Malta). Thus, results for countries with islands of small size would slightly change.

Ranking	Country	ICC[1]	Median	Maximum	Mean	Std Dev.
	Europe		**1543**	**83479**	**2849.96**	**4741.27**
	Europe28		**1513**	**54294**	**2539.32**	**3508.17**
1	Belgium	BE	565	6436	785.59	757.64
2	Luxembourg	LU	583	4560	794.69	735.68
3	Netherlands	NL	873	13024	1300.04	1502.07
4	Czech republic	CZ	901	10169	1228.56	1166.19
5	United Kingdom	GB-ND	939	20334	1694.28	2224.41
6	Germany	DE	992	11950	1358.64	1304.25
7	Croatia	HR	1011	10890	1448.82	1438.23
8	Denmark	DK	1025	12264	1422.30	1374.46
9	Slovenia	SI	1025	10223	1380.91	1288.84
10	Liechtenstein	LI	1060	5408	1451.03	1281.61
11	Ukraine	UA	1096	22500	1523.20	1592.70
12	Hungary	HU	1159	10630	1540.88	1401.27
13	Moldova	MD	1192	9190	1484.90	1247.54
14	Ireland	IE	1234	13144	1677.31	1579.85
15	Cyprus	CY	1237	15140	1766.36	1768.91
16	Italy	IT	1358	21955	2037.33	2132.04
17	France	FR	1394	22040	2121.17	2287.91
18	Greece	GR	1443	36176	2103.20	2296.25
19	Switzerland	CH	1503	17952	2315.98	2376.10
20	Romania	RO	1595	38181	2345.24	2665.37
21	Poland	PL	1686	16174	2242.81	2024.56
22	Portugal	PT	1708	20539	2414.21	2347.30
23	Sweden	SE	1735	54294	4156.82	6681.55
24	Bulgaria	BG	1750	17862	2364.78	2229.73
25	Austria	AT	1812	18752	2654.19	2657.55
26	Serbia	RS	1833	16813	2457.38	2249.60
27	Slovakia	SK	1860	14502	2454.31	2208.29
28	Republic of Macedonia	MK	1882	15093	2453.27	2142.14
29	Spain	ES	1900	31727	2660.43	2648.00
30	Andorra	AD	1930	9253	2290.22	1754.44
31	Lithuania	LT	2360	19227	3033.88	2609.37
32	Latvia	LV	2901	19872	3528.01	2863.85
33	Finland	FI	2944	49202	4841.46	5830.66
34	Estonia	EE	2951	31433	4078.30	3954.39
35	Norway	NO	3326	56455	5653.55	6751.04
36	Iceland	IS	9722	83479	16497.40	17510.10

[1] International Country Codes used in EuroGlobalMap (EGM) dataset.

Table S3. Attribution of land covers from the SIOSE project to built-up areas and impervious infrastructure.

Artificial cover types	Class	Class (Spanish)[a]	Label	Included in U.S.G.[b]	Included in F.G.[c]
Simple covers					
	Building	Edificación	EDF	Yes	Yes
	Green space	Zona verde artificial y arbolado urbano	ZAU	Yes if size ≤ 4ha	Yes if size ≤ 4ha
	Artificial water body	Lámina de agua artificial	LAA	No	Yes
	Street boundaries without vegetation, parking place	Vial, aparcamiento o zona peatonal sin vegetación	VAP	No	Yes
	Other constructions	Otras construcciones	OCT	Yes	Yes
	Land without current use	Suelo no edificado	SNE	No	No
	Earthwork and landfill sites	Zonas de extracción o vertido	ZEV	No	No
Predefined compound covers (compound by simple covers)[d]					
	Farmhouse	Asentamiento agrícola-residencial	AAR	Yes	Yes
	Continuous urban area – urban centre	Urbano mixto – casco	UCS	Yes	Yes
	Continuous urban area – expansion area	Urbano mixto – ensanche	UEN	Yes	Yes
	Discontinuous urban area	Urbano mixto – discontinuo	UDS	Yes	Yes
	Organized industrial estate	Polígono industrial ordenado	IPO	Yes	Yes
	Disorganized industrial estate	Polígono industrial sin ordenar	IPS	Yes	Yes
	Isolated industry	Industria aislada	IAS	Yes	Yes
	Agricultural and livestock development	Agrícola/Ganadero	PAG	Yes	Yes
	Forestry	Forestal	PFT	Yes if EDF ≥ 50%[e]	Yes if EDF ≥ 50%
	Mining, gravel pits, etc.	Minero extractivo	PMX	Yes if EDF ≥ 50%	Yes if EDF ≥ 50%
	Fish farm	Piscifactoría	PPS	Yes if EDF ≥ 50%	Yes if EDF ≥ 50%
	Commercial unit	Comercial y oficinas	TCO	Yes	Yes
	Hotel development	Complejo hotelero	TCH	Yes	Yes
	Leisure facilities	Parque recreativo	TPR	Yes	Yes
	Campsite	Camping	TCG	Yes if EDF ≥ 50%	Yes if EDF ≥ 50%
	Administrative or institutional facility	Equipamiento/Dotacional – Administrativo/institucional	EAI	Yes	Yes
	Hospital or health center	Equipamiento/Dotacional – sanitario	ESN	Yes	Yes
	Cemetery	Equipamiento/Dotacional – cementerio	ECM	Yes	Yes
	Education center	Equipamiento/Dotacional – educación	EDU	Yes	Yes
	Penitentiary	Equipamiento/Dotacional – penitenciario	EPN	Yes	Yes
	Religious building	Equipamiento/Dotacional – religioso	ERG	Yes	Yes
	Cultural center	Equipamiento/Dotacional – cultural	ECL	Yes	Yes
	Sport facilities	Equipamiento/Dotacional – deportivo	EDP	Yes if ZAU ≤ 4ha[f]	Yes if ZAU ≤ 4ha
	Golf club	Equipamiento/Dotacional – campo de golf	ECG	No	No
	Urban park	Equipamiento/Dotacional – parque urbano	EPU	Yes if ZAU ≤ 4ha	Yes if ZAU ≤ 4ha
	Road network and facilities	Infraestructuras – red viaria	NRV	Yes if EDF ≥ 50%	Yes
	Railway network and facilities	Infraestructuras – red ferroviaria	NRF	Yes if EDF ≥ 50%	Yes

Port	Infraestructuras – portuario	NPO	Yes	Yes
Airport	Infraestructuras – aeroportuario	NAP	Yes	Yes
Wind power plant	Infraestructuras – energía eólica	NEO	Yes if EDF ≥ 50%	Yes if EDF ≥ 50%
Solar power plant	Infraestructuras – energía solar	NSL	Yes if EDF ≥ 50%	Yes if EDF ≥ 50%
Nuclear power plant	Infraestructuras – energía nuclear	NCL	Yes	Yes
Power plant	Infraestructuras – energía eléctrica	NEL	Yes	Yes
Thermal power station	Infraestructuras – energía térmica	NTM	Yes	Yes
Water power station	Infraestructuras – energía hidroeléctrica	NHD	Yes	Yes
Pipeline	Infraestructuras – gaseoducto/oleoducto	NGO	Yes if EDF ≥ 50%	Yes
Transmitter station, RADAR station, etc.	Infraestructuras – telecomunicaciones	NTC	Yes if EDF ≥ 50%	Yes if EDF ≥ 50%
Sewage treatment plant	Infraestructuras – depuradoras y potabilizadoras	NDP	Yes	Yes
Desalinisation plant	Infraestructuras – desalinizadoras	NDS	Yes	Yes
Channel	Infraestructuras – conducciones y canales	NCC	Yes if EDF ≥ 50%	Yes
Dump	Infraestructuras – vertederos y escombreras	NVE	Yes	Yes
Waste treatment plant	Infraestructuras – plantas de tratamiento	NPT	Yes	Yes
No predefined compound covers	*(compound by simple and compound covers)*[g]			
Association	Asociación	A	Yes	Yes
Irregular mosaic	Mosaico irregular	I	Yes	Yes
Regular mosaic	Mosaico regular	R	Yes	Yes

[a] The Spanish name of the class is provided because the source database is in Spanish.

[b] Urban sprawl geometry

[c] Fragmentation geometry

[d] The polygons of predefined compound covers were incorporated to the layers of urban sprawl geometry and fragmentation geometry if at least 50 % of their surface was occupied by simple covers that met the corresponding inclusion criteria.

[e] The polygons of this class were selected only when 50 % of their surface was occupied specifically by buildings (simple class with label EDF).

[f] The polygons of this class were selected only when the surface of green space (simple class with label ZAU) was lower than 4 ha.

[g] The polygons of no predefined compound covers were incorporated to the layers of urban sprawl geometry and landscape fragmentation geometry if at least 50 % of their surface was occupied by simple or predefined compound covers that met the corresponding inclusion criteria.

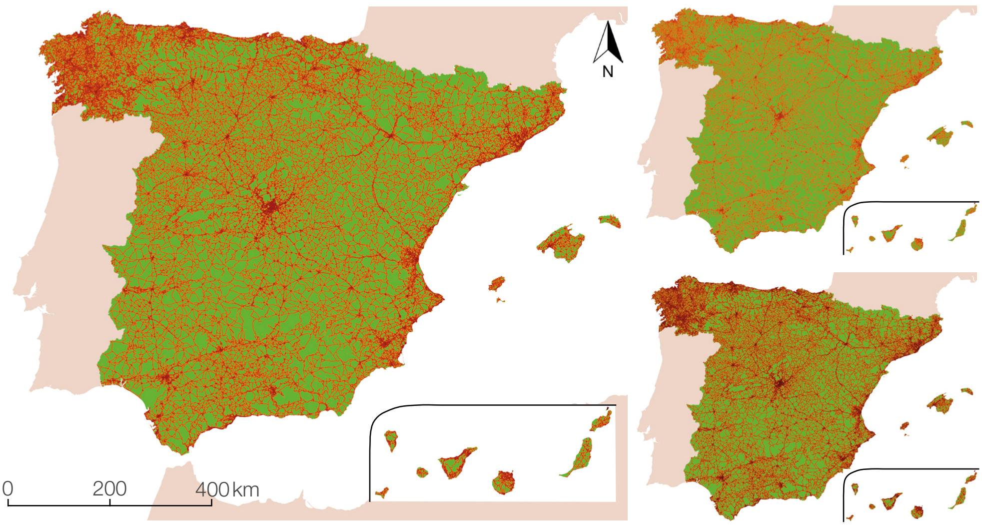
Table S5. Summary of the distances to the nearest built-up area, transport infrastructure, and all impervious infrastructure combined based on Corine Land Cover (2006) classes. (The results for artificial cover types and water bodies are not presented.)

Level[a]	Label Code	Label name	Built-up areas range (km)	Built-up areas median (km)	Transport infrastructure range (km)	Transport infrastructure median (km)	All impervious infrastructure range (km)	All impervious infrastructure median (km)
L1	2	**Agricultural areas**						
L2	21	*Arable land*	0-13.050	1.323	0-16.195	0.724	0-9.972	0.560
L3	211	Non-irrigated arable land	0-13.050	1.463	0-16.195	0.783	0-9.972	0.646
L3	212	Permanently irrigated land	0-10.775	0.813	0-11.761	0.500	0-7.397	0.320
L3	213	Rice fields	0-6.601	1.161	0-10.866	1.124	0-3.408	0.255
L2	22	*Permanent crops*	0-10.954	1.260	0-11.248	0.630	0-6.945	0.496
L3	221	Vineyards	0-10.038	1.612	0-8.166	0.697	0-6.945	0.594
L3	222	Fruit trees and berry plantations	0-10.954	0.684	0-8.772	0.411	0-6.869	0.279
L3	223	Olive groves	0-10.771	1.442	0-11.248	0.735	0-6.486	0.599
L2	23	*Pasture*	0-9.838	0.653	0-9.827	0.255	0-8.637	0.212
L2	24	*Heterogeneous agricultural areas*	0-15.344	1.288	0-12.447	0.658	0-10.358	0.530
L3	241	Annual crops associated with permanent crops	0-6.146	1.077	0-5.790	0.495	0-4.044	0.422
L3	242	Complex cultivation patterns	0-11.622	0.845	0-10.402	0.429	0-7.597	0.331
L3	243	Land principally occupied by agriculture, with significant areas of natural vegetation	0-12.466	1.179	0-10.352	0.636	0-10.358	0.536
L3	244	Agro-forestry areas	0-15.344	2.193	0-12.447	1.277	0-8.981	0.966

Level[a]	Label Code	Label name	Built-up areas range (km)	Built-up areas median (km)	Transport infrastructure range (km)	Transport infrastructure median (km)	All impervious infrastructure range (km)	All impervious infrastructure median (km)
L1	3	**Forest and semi-natural areas**						
L2	31	*Forests*	0-15.436	1.935	0-12.056	1.124	0-10.993	1.004
L3	311	Broad-leaved forest	0-15.436	1.794	0-12.056	1.081	0-10.478	0.959
L3	312	Coniferous forest	0-14.287	2.280	0-11.97	1.320	0-10.993	1.188
L3	313	Mixed forest	0-11.561	1.339	0-8.98	0.753	0-8.927	0.660
L2	32	*Scrub and/or herbaceous vegetation associations*	0-15.444	1.991	0-13.329	1.190	0-13.324	1.033
L3	321	Natural grasslands	0-14.469	1.794	0-13.329	1.023	0-13.324	0.851
L3	322	Moors and heathland	0-11.744	1.576	0-10.406	0.945	0-10.405	0.868
L3	323	Sclerophyllous vegetation	0-15.306	2.036	0-12.751	1.250	0-11.172	1.094
L3	324	Transitional woodland-shrub	0-15.444	2.153	0-13.011	1.277	0-11.464	1.110
L2	33	*Open spaces with little or no vegetation*	0-14.522	2.100	0-13.400	1.541	0-13.395	1.271
L3	331	Beaches, dunes, sands	0-9.493	0.933	0-12.441	0.566	0-7.398	0.423
L3	332	Bare rocks	0-14.522	3.124	0-13.400	2.590	0-13.395	2.364
L3	333	Sparsely vegetated areas	0-13.318	1.958	0-12.35	1.442	0-12.35	1.161
L3	334	Burnt areas	0-11.552	2.312	0-7.680	1.214	0-7.122	1.108
L3	335	Glaciers and perpetual snow	0-10.645	4.727	0-9.246	4.854	0-9.241	4.717
L1	4	**Wetlands**						
L2	41	*Inland wetlands*	0-9.936	3.679	0-16.566	6.318	0-7.176	1.100
L3	411	Inland marshes	0-9.936	3.694	0-16.566	6.392	0-7.176	1.095
L3	412	Peat bogs	0.045-7.447	2.430	0-6.826	2.128	0-5.444	1.745
L2	42	*Maritime wetlands*	0-9.871	0.865	0-10.698	0.771	0-5.312	0.450
L3	421	Salt marshes	0-9.709	0.777	0-10.698	0.720	0-5.312	0.414
L3	422	Salines	0-9.871	1.125	0-9.449	1.005	0-3.603	0.564
L3	423	Intertidal flats	0-2.565	0.375	0-2.375	0.294	0-2.013	0.212

[a] Corine Land Cover uses a hierarchical scheme of three levels to describe land cover.

a)
MSA birds



b)
MSA mammals

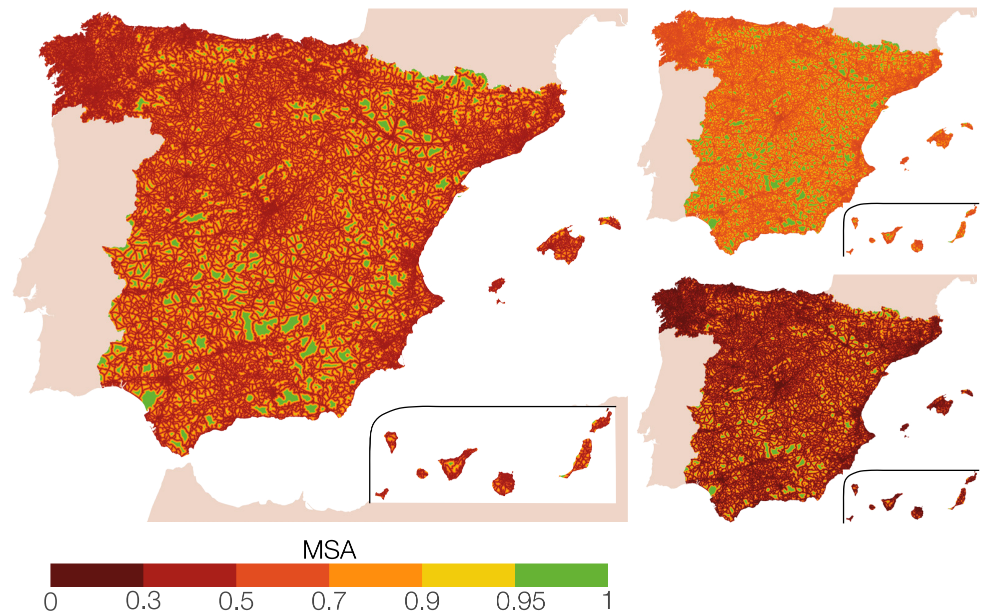
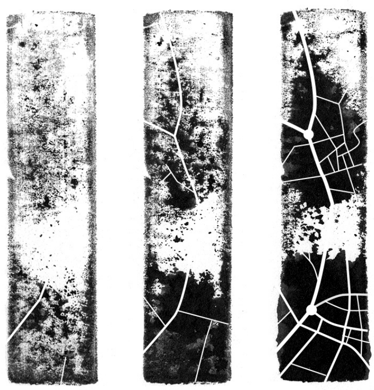


Figure S1. Predicted mean species abundance (*MSA*) of birds (a) and mammals (b) across Spain according to proximity to transport infrastructure, based on the effect distance-decay curves fitted for empirical data by Benítez-López et al. (2010). The adjacent smaller maps represent the upper (up) and lower (down) confidence intervals. MSA layers were reclassified into 6 effect intensity zones for representation.

Chapter

Capítulo



La discordancia entre dispersión urbanística y la fragmentación del paisaje a múltiples escalas crea espacios de oportunidad para la conservación y el desarollo

Resumen

Contexto. La dispersión de la urbanización y el desarrollo de infraestructuras de transporte son la fuerza motriz de la fragmentación del paisaje y el consumo de superficie de suelo. El conocimiento que se tiene de cómo estos factores interaccionan para dar forma a la fragmentación del paisaje es todavía limitado. Sin embargo, se asume una fuerte correlación entre la dispersión de la urbanización y la fragmentación del paisaje.
Objetivos. El objetivo general es comprobar la fuerza, la variación espacial y la dependencia de la escala de la relación entre los patrones de dispersión de la urbanización y fragmentación del paisaje (‘*relación dispersión-fragmentación*’). También proponemos un marco ampliado de las relaciones entre la dispersión urbanística, la expansión de infraestructuras de transporte y la fragmentación del paisaje.
Métodos. Cuantificamos los patrones espaciales de dispersión urbanística y fragmentación del paisaje para la España peninsular a múltiples escalas. Tras esto, ajustamos modelos de regresión globales y modelos de regresión ponderados geográficamente con indicadores de fragmentación del paisaje y dispersión urbanística a varias escalas.
Resultados. En los modelos globales, la mayor parte de la variación en los valores de fragmentación de paisaje no se puede explicar con los indicadores de dispersión urbanística (casi el 80% en promedio). Los modelos locales muestran un mejor desempeño con un promedio del 37% de la varianza aún no explicada. La contribución de la dispersión urbanística a la fragmentación del paisaje varía espacialmente y depende de la escala, con un mejor ajuste a grandes escalas y a niveles jerárquicos más elevados.
Conclusiones. Nuestra investigación revela tres características críticas de la relación dispersión-fragmentación: No es predominante, varía espacialmente y con la escala. Proponemos varios mecanismos que pueden explicar esta discordancia: la escala, el retraso temporal del desarrollo, su distribución espacial y otras variables externas incluyendo conexiones a larga distancia. Estas discordancias espaciales proporcionan espacios de oportunidad para la conservación mediante mejores estrategias de desarrollo.

Torres, A., Jaeger, J.A.G., Alonso, J.C. Multi-scale mismatches between urban sprawl and landscape fragmentation create windows of opportunity for conservation development. Under review in Landscape Ecology.

Multi-scale mismatches between urban sprawl and landscape fragmentation create windows of opportunity for conservation development

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Abstract

Context. Urban sprawl and the expanding transportation infrastructure drive land consumption and landscape fragmentation, causing species loss and environmental deterioration. Current understanding of how these drivers interact to shape landscape fragmentation is still poor. However, a strong correlation between urban sprawl and landscape fragmentation patterns is assumed.

Objectives. The overarching objective is to test the strength, non-stationarity, and scale-dependency of the relationship between urban sprawl and landscape fragmentation patterns ('*sprawl-fragmentation relationship*'). Then, we propose an extended framework for the links between urban sprawl, expansion of transport infrastructure, and landscape fragmentation.

Methods. We quantified spatial patterns of urban sprawl and landscape fragmentation for mainland Spain at multiple scales. We then fitted global regression models and geographically weighted regression models with metrics of landscape fragmentation and urban sprawl at multiple scales.

Results. Most variation in landscape fragmentation values (almost 80% on average) is not explained by urban sprawl metrics through global modeling. Local models show substantial improvements in model performance, with an average of 37% of the variance remaining unexplained. The contribution of urban sprawl to landscape fragmentation patterns varies locally and depends on scale, with higher contribution at coarser scales and at higher organizational levels.

Conclusions. Our investigation revealed three critical characteristics of the sprawl-fragmentation relationship: it does not prevail, is non-stationary, and scale-dependent. We propose four mechanisms that may have resulted in this

mismatch: scale, time-lagged development, spatial arrangement of development, and other external variables including teleconnections. These spatial mismatches provide windows of opportunity for conservation through better development strategies.

KEYWORDS Effective mesh density, landscape conservation, land scarcity, non-stationarity, rural sprawl, scale dependency, Spain, spatial scale, urban dispersion, urban development.

Introduction

Land is needed to fulfill growing food demands, producing renewable energy, maintaining ecosystem services, urban-industrial uses, transport, material extraction, but also for leisure, recreation, and nature conservation. All of these needs compete for land, whose increasing scarcity is strongly underrated (Haber 2007). Development of urban areas and transport infrastructures will transform cities and landscapes globally at an unprecedented pace in the next decades (Seto et al. 2012a), with urban sprawl becoming increasingly common and not only restricted to metropolitan areas (Brown et al. 2005; EEA 2006; Inostroza et al. 2013). Throughout this article, we consider urban sprawl along a continuous gradient rather than distinguishing only urban or rural sprawl from non-sprawl.

The pressure from rapid urban sprawl and expanding transport networks drives environmental change at multiple scales (Grimm et al. 2008) and represent a growing threat to human health, biodiversity, and the provisioning of ecosystem services (Forman et al. 2003; Whitmee et al. 2015). Yet, urban development and transport infrastructure impact landscapes through synergistic processes. However, the understanding of the interactions between these and other drivers of landscape change is still limited (Brook et al. 2008). Landscape fragmentation, for example, results from the interaction between urban development and transport infrastructure expansion, and is one of the most widely recognized effects of anthropogenic development (Theobald et al. 1997; Trombulak and Frissell 2000; Laurance et al. 2009).

How does urban sprawl and transport infrastructure interact to shape landscape fragmentation? It is widely assumed that urban sprawl and the development of the transport network influence each other, interacting both as driver and catalyst, in the form of a feedback loop (Fig. 1). Consequently, the assumption that sprawl and fragmentation patterns are highly correlated is getting increasingly common (e.g., Siedentop and Fina 2010; Selva et

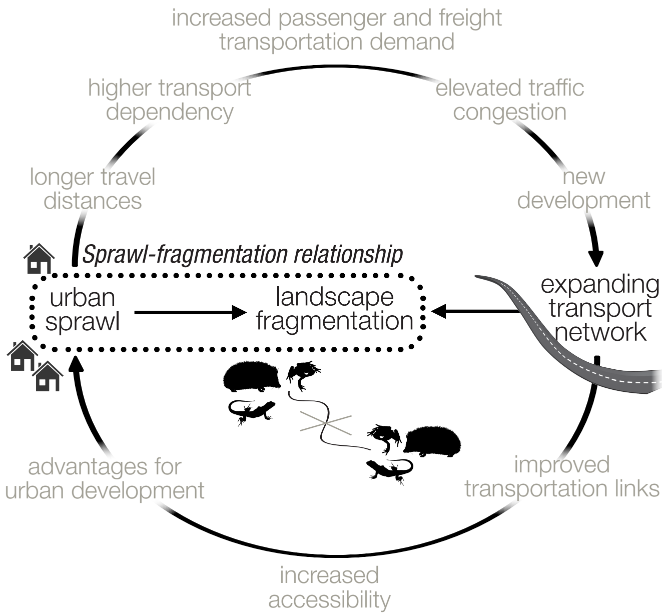


Figure 1. Feedback loop between urban sprawl and the transport network. The growing spatial dispersion of activities and dwellings shapes travel demands of both people and freight by increasing travel distances (Bento et al. 2005; Vance and Hedel 2007; Travisi et al. 2010). The resulting high levels of traffic congestion trigger demands for new transport infrastructure. In turn, new transport infrastructure influence urban development patterns by enhancing accessibility of undeveloped areas, encouraging the development of the urban fringe and the establishment of economic activities (Handy 2005; Hawbaker et al. 2006). Since both drivers contribute to landscape fragmentation, the assumption of a high correlation between urban sprawl and landscape fragmentation patterns ("*sprawl-fragmentation relationship*") seems intuitive.

al. 2011). A few studies, mostly located in metropolitan areas, explored the relationship between sprawl and fragmentation (Clark et al. 2009), though most of them refer to fragmentation of urban areas (e.g., Irwin and Bockstael 2007; Inostroza et al. 2013), whereas Hawbaker et al. (2005) analysed the correlation between road and housing density. In addition, most definitions of urban sprawl mix causes and consequences of urban sprawl into the description of the sprawl pattern per se (Jaeger et al. 2010b). Consequently, the degree of landscape fragmentation, which is a cause or consequence of sprawl, have been frequently used to measure urban sprawl, and conversely, some metrics of sprawl are assumed to be valid surrogates of the ecological impacts of transport development like landscape fragmentation (Theobald et al. 1997; Schupp 2005; Hawbaker et al. 2006; Jaeger et al. 2008; Selva et al.

2011), adding more confusion to the issue. Despite a long history of landscape ecologists discussing urbanization and landscape fragmentation patterns, the current knowledge on the sprawl-fragmentation relationship is partial and ambiguous and can lead to misunderstandings when comparing results from different studies. Therefore, it is desirable to test this qualitative assumption by explicitly (1) considering the spatial arrangement of built-up areas, (2) including transport infrastructure and built-up areas in the fragmentation analysis, and (3) characterizing urban sprawl or urbanization patterns in a quantitative way.

Further misunderstanding can arise in the discussion of the sprawl-fragmentation relationship if scale-effects are ignored. Drivers of landscape change like urban sprawl or infrastructure development operate and interact over a wide-range of spatial scales and there are often hierarchical linkages among them (Wu et al. 2006). In addition, the analysis of urban sprawl has its own scale, captured by the maximum distance at which dispersion of built-up areas is measured (Jaeger et al. 2010a). Although there are general scaling rules, the behavior of the sprawl-fragmentation relationship across scales may differ significantly when different components of scale are examined.

Here, we tested the hypothesis that sprawl and fragmentation patterns strongly match, based on spatially explicit quantifications of urban sprawl and landscape fragmentation gradients in Spain. We examined the spatial non-stationarity of the sprawl-fragmentation relationship, as well as the potential of different dimensions of urban sprawl to explain the variation in landscape fragmentation patterns. A multi-scale assessment was applied to investigate the scale-dependencies of the sprawl-fragmentation relationship by modifying both the spatial scale of the reporting units and the scale of urban sprawl measurement. Finally, we discuss the potential mechanisms that lead to a widespread mismatch between the spatial patterns of urban sprawl and landscape fragmentation by presenting an extended framework for the sprawl-fragmentation relationship.

Further proliferation of urban sprawl and expanding transport infrastructure will exacerbate many of the problems they have already created, including landscape fragmentation. This is the first study that explicitly analyzes the sprawl-fragmentation relationship. It leads to enhanced understanding of the theoretical and empirical relationships between drivers of landscape change. Such knowledge is essential for guiding land-use planning and defining sustainable development strategies as well as for informing decision-making in regional planning and management (Jaeger et al. 2008).

Methods

STUDY AREA AND REPORTING UNITS

The study area encompasses mainland Spain (Fig. S1), which covers 498,749 km^2 and supports a human population of 43.5 million (Spanish Statistical Office; Population Census 2011). Transport infrastructure and built-up areas constitute a major source of disturbance: 50% of the land area in Spain is within 718 m of one of these fragmenting elements (Torres et al. subm.). The mountainous relief and the varied forms of human land use resulted in landscapes that harbor an extraordinary biodiversity, while allowing for wide gradients of urban sprawl and landscape fragmentation to be well represented (PBL 2008; EEA and FOEN 2011).

Landscape metrics were calculated and analyzed in relation to defined spatial units. We applied a multi-scale assessment approach in which we considered three types of spatial units with nested spatial scales within each of them: political boundaries, ecological boundaries, and regular grids (Fig. S1). All of them are meaningful organizational units that are widely used for planning, management, and conservation purposes, but their boundaries correspond to different criteria. Municipalities are nested within provinces. Landscapes are nested hierarchical entities with major landscape associations containing multiple types of landscapes, which in turn comprise landscape units at finer spatial scales (Mata and Sanz 2003). We also included river basins because the assessment of some important ecosystem services is commonly performed at this boundary, even though this watershed boundary is a non-nested spatial scale. Municipality, province, landscape, and watershed boundaries were obtained from MAGRAMA (Ministry of Agriculture, Food, and Environment). Finally, grids of 50 x 50 km, 10 x 10 km, 5 x 5 km, and 2 x 2 km were generated in ArcGIS 10.1 (ESRI). Cells that had more than 50% of their surface in a neighboring country or in the sea were excluded. This approach resulted in a total of 10 types of reporting units.

QUANTIFICATION OF URBAN SPRAWL

Delineation of urban areas (Table S1) was based on the Spanish Land Cover and Use Information System (SIOSE, 1:25,000 scale; National Geographic

Institute of Spain 2005), which is the most accurate cartography to record low-density sprawl in Spain. 'Urban areas' denote patches of built-up area, irrespective of their use. Only those traffic areas that are located within the settlements were included.

Quantification of urban sprawl applied a set of metrics that characterize the pattern of urban development from a geometric point of view: *proportion of urban area* (*PUA*), *degree of urban dispersion* (*DIS*), and *degree of urban permeation* (*UP*). Urban sprawl increases with both, higher amount of urban area and higher dispersion (Jaeger et al. 2010b). *DIS* quantifies the spatial arrangement of urban areas, and is based on the distances between any two points within the urban areas in the reporting unit (for all possible pairs of points within and between urban patches). *DIS* is weighted with an effort function so that the farther apart the two points from each other, the higher their contribution to *DIS*, and the higher the effort required to connect them (Jaeger et al. 2010a). This is expressed in urban permeation units (UPU) per m^2 of urban area. The minimum possible value of *DIS* (0 UPU/m^2) is found when there is no urban area in the reporting unit. The maximum values of *DIS* are reached when each urban patch is located away (evenly dispersed) from all other urban patches (according to the scale of analysis of sprawl; see below). Finally, *UP* describes the degree to which a landscape is permeated by urban area by integrating the contribution of the amount of urban area and its degree of dispersion. The formula for *UP* is as follows:

$$UP = A_{urban} / A_{reporting\ unit} \cdot DIS = PUA \cdot DIS,$$

where A_{urban} is the total amount of urban area within the reporting unit and $A_{\text{reporting unit}}$ is the size of the reporting unit. *UP* is expressed in urban permeation units per m^2 of land (UPU/m^2). When new buildings are added within the existing urban areas (densification), the values of these metrics do not change. Urban sprawl metrics were checked for multicollinearity using Spearman's correlation.

The effect of changing the scale of urban sprawl measurement within reporting units is analyzed by modifying the maximum distance up to which point-to-point distances are measured, i.e., the horizon of perception (*HP*) (Jaeger et al. 2010a). For example, at a small *HP*, the urban areas may appear to be evenly distributed, whereas at a large *HP* it may become apparent that the urban areas are clumped (Fortin and Dale 2005). With increasing *HP*, the values of the sprawl metrics increase, as more urban area is considered. We used an *HP* of 2 km and 5 km for calculating *DIS* (DIS_2, DIS_5) and *UP* (UP_2, UP_5) and applied the cross-boundary connections procedure (Moser et al. 2007), where the settlement pattern outside the reporting unit but within the *HP* also influences the values of the metrics. Both distances are recommended as *HP*, since they cover a relatively wide range of urban sprawl and have been supported in previous studies (Wissen Hayek et al. 2011; Schwick et al. 2012; Jaeger and Schwick 2014).

QUANTIFICATION OF LANDSCAPE FRAGMENTATION

We delineated a map of fragmenting elements for the whole of peninsular Spain, considering fragmentation caused by anthropogenic barriers, mainly: paved roads, railways, and urban areas (Jaeger et al. 2008). The map combined linear and 2-dimensional features. Delineation of 2-dimensional features was based on the SIOSE project, considering all the land cover types contributing to urban sprawl (i.e., built-up areas), but also others that limit species movement or reduce recreational opportunities (e.g., parking lots). We considered paved linear transport infrastructure from the BCN200 dataset (1:200,000 scale; National Geographic Institute of Spain 2011) that were built or under construction, excluding sections in which those infrastructures go through tunnels or have a viaduct section (with a length longer than 200 m), and buffered them based on road and railway classes to reflect the occupied surface (Table S2).

We applied the *effective mesh size* metric (m_{eff}) (Jaeger 2000) to quantify landscape fragmentation, following the cross-boundary-connections procedure in which reporting unit boundaries do not fragment the landscape (Moser et al. 2007). This metric is based on the probability that any two points chosen randomly in an area are connected and are not separated by any barriers. This leads to the formula:

$$m_{\text{eff}}^{\text{CBC}}(\text{unit } j) = \frac{1}{A_{tj}} \sum_{i=1}^{n} A_{ij} \cdot A_{ij}^{\text{cmpl}},$$

where n is the number of remaining patches i (not urban), A_{tj} is the total area of reporting unit j, A_{ij} is the area of patch i inside of reporting unit j and A_{ij}^{cmpl} is the complete area of patch i including the area outside the boundaries of reporting unit j. The smaller the m_{eff}, the more fragmented the landscape. The largest possible value of m_{eff} is the size of the region studied when the landscape is unfragmented. The smallest value of 0 km² indicates complete fragmentation, i.e., no suitable area left. However, the m_{eff} measure reacts more slowly to increasing fragmentation as it approaches 0 km^2. To avoid this effect, we also calculated the *effective mesh density* $s_{eff} = 1/m_{eff}$, which is more suitable for detecting and comparing slopes in graphs (Jaeger 2000, 2002; Jaeger et al. 2007). The value of s_{eff} was expressed as the effective number of meshes per 1000 km^2. The higher number of meshes, the more fragmented the landscape.

STATISTICAL ANALYSIS

We first fitted global regressions using ordinary least squares (OLS) with log-transformed s_{eff} as response variable (ln of effective number of meshes per 1000 km^2 * 1000 km^2 + 1 to avoid any negative values or inconsistencies with the units) and single sprawl metrics (*PUA*, DIS_2, DIS_5, UP_2, and UP_5). We also performed multivariate global regressions considering the two dimensions of urban sprawl (*PUA* and *DIS*) together, which may better predict landscape fragmentation than any single sprawl metric. To determine empirically whether and how the sprawl-fragmentation relationship changes with scale, we used a separate model for each of the reporting units and *HP*s. A total of 70 OLS models were compared. Outliers and influential points were investigated by examining standard regression diagnostics (residual vs. prediction plot, Q-Q plots, and Cook's distance).

Incorporating non-stationarity is useful to reveal spatial structures in data and relationships between patterns at multiple scales (Da Silva Cassemiro et al. 2007). We used geographically weighted regression (GWRs; Fotheringham et al. 2002) to explore regional variations in the sprawl-fragmentation relationship across the study area. GWR generates a local regression model by using surrounding observations within a particular distance (bandwidth) of the focal unit and allowing the model's parameters to vary locally across the study area. We adopted an adaptive Gaussian kernel based on the minimization of the Akaike Information Criterion (AIC) to calibrate the spatial weighting scheme according to an inverse-distance linear function (Fotheringham et al. 2002). Due to limited sample size, we did not include the coarsest scales (provinces and landscape associations) in the multivariate GWR models. A total of 66 GWR models were compared. We mapped the local model performance (r^2), local parameter estimates, as well as over- and underpredictions from the GWR models to determine if spatial clustering patterns existed. To investigate the effect of changing scale on the predictive ability of urban sprawl metrics, we plotted changes in global and local r^2 across spatial extents, spatial configurations, and scales of urban sprawl measurement.

We assessed spatial autocorrelation for the residuals of the OLS and GWR models using Moran's I statistic with inverse distance weighting and Euclidean distance calculation (Cliff and Ord 1981). R (Team 2011) and ArcGIS 10.1 (ESRI) were used for all spatial and statistical analyses.

Results

How much variation in landscape fragmentation can be explained by urban sprawl?

The combined results of global models showed that urban sprawl metrics accounted on average for 0.20 ± 0.07 SD of the variance in landscape fragmentation (Table S3), with the best global model explaining up to 0.43 of variation. Local models showed substantial improvements in model performance over all global models, corresponding to an average of 0.66 ± 0.16 SD of the variance in landscape fragmentation (Table S3), with the best local model explaining up to 0.91 of variation. Together with the spatial variations in model performance, steepness, and even in the sign of the relationship across the study area (Fig. S2 to S7), these findings indicate that the relationship between patterns of urban sprawl and landscape fragmentation is strongly non-stationary. Furthermore, analysis of spatial autocorrelation in the residuals also supported the better fit of the local models (Table S3), as the mean Moran's I was 0.53 ± 0.22 SD for the global models and 0.24 ± 0.21 SD for the local models, suggesting that spatial autocorrelation in the residuals of local models was weak, although for some units it was still significant.

Regarding the parameter estimates, the intercept ranged between 2.417 and 11.947 in the global models (m_{eff}: 6.5 to 97,922.4 km^2), and between 3.753 and 12.108 in the local models (m_{eff}: 5.5 to 4,103.5 km^2) (Tables S4 and S5). A positive relationship between urban sprawl values and landscape fragmentation levels is predicted, i.e., landscape fragmentation overall grows with increasing *PUA*, *DIS*, or *UP*. Nonetheless, the local models revealed that a considerable proportion of the study area, ranging from 0% to 24.3% (depending on the metric and the scale), exhibited a negative slope (Fig. S2 to S7).

According to the spatial variation in the regression residuals from global models (Fig. S8 to S14), the largest overestimations of landscape fragmentation were found at the highest elevations (e.g., mountainous areas of Pyrenees, Cantabrian Range, and Sierra Morena Range). In contrast, the areas where landscape fragmentation was underestimated were more widely distributed, depending on the metric and the scale. By allowing the parameter estimates to vary locally, these deviations disappeared in the local models.

WHAT METRIC OF URBAN SPRAWL BEST EXPLAINS VARIATION IN LANDSCAPE FRAGMENTATION?

The explanatory strength of the sprawl metrics varied considerably between modeling techniques. Nonetheless, the model performance of *DIS*-models was lower on average (mean ± SD = 0.35 ± 0.22 of variation) than of the *PUA*- and *UP*-models (mean ± SD = 0.49 ± 0.31 of variation; Table S3). In contrast, local *PUA*- and *UP*-models predicted a negative relationship between urban sprawl and landscape fragmentation for a larger area (mean ± SD = 10.51 ± 8.55%) than *DIS*-models (mean ± SD = 3.04 ± 4.22%), and predicted a higher level of landscape fragmentation at zero urban sprawl than *DIS*-models.

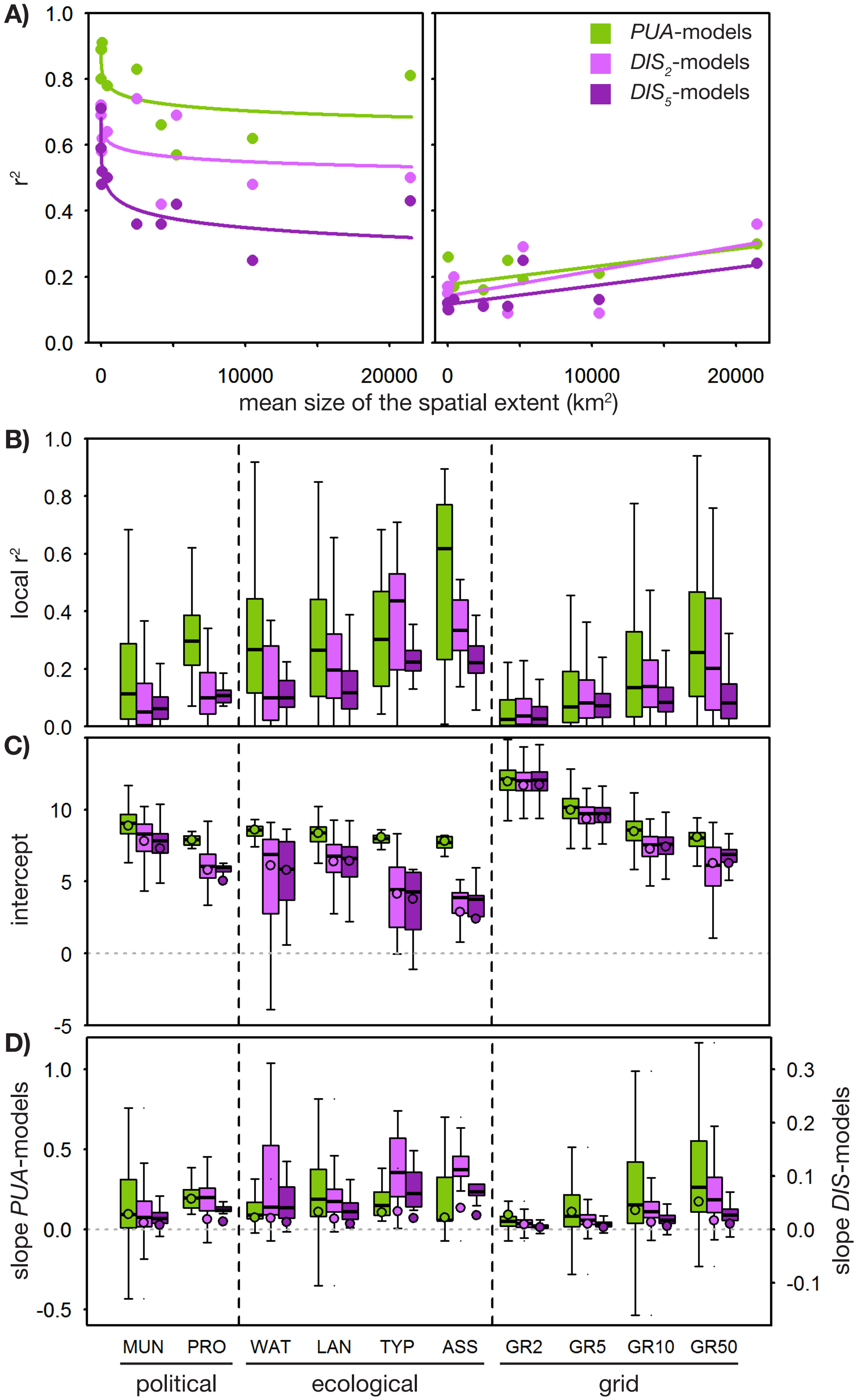
When including both *PUA* and *DIS*, the global analyses showed considerably stronger relationships between urban sprawl and landscape fragmentation patterns than any of the univariate models across scales (mean ± SD percentage variation explained in univariate models = 0.18 ± 0.06 of variation; in multivariate models = 0.26 ± 0.06; Table S3). However, using GWR modeling, *PUA*- and *UP*-models still exhibited a notably better fit on average (mean ± SD = 0.78 ± 0.12 of variation) than the *DIS*-models and the multivariate models (*DIS*-models: mean ± SD = 0.54 ± 0.14 of variation; multivariate models: mean ± SD = 0.60 ± 0.10 of variation; Table S3).

We recorded a high collinearity between *PUA* and *UP* (Table S6), which is also supported by the similarity in their spatial structure (Fig. S2, S5, and S6). In contrast, the correlations between *DIS* and *PUA* or *UP* were weaker and differed with the scale of urban sprawl (when *HP* increased, the correlation became weaker; $DIS_2 \sim PUA$: mean rs± SD = 0.86± 0.07; $DIS_5 \sim PUA$: mean rs± SD = 0.61± 0.22; $DIS_2 \sim UP_2$: mean rs± SD = 0.90± 0.05; $DIS_2 \sim UP_5$: mean rs± SD = 0.67± 0.18), as well as with the reporting unit (Table S6). Yet, we did not perform a multiple model with *PUA* or *DIS* and *UP*.

SCALE-EFFECTS

We found a strong influence of spatial scale on both the strength and the shape of the sprawl-fragmentation relationship. Regarding the strength, we identified a negative logarithmic scaling curve between the extent of the reporting units and model performance of GWR models (strength of the fit: r^2 *PUA* = 0.37, r^2 DIS_2 = 0.29, r^2 DIS_5 = 0.77; r^2 UP_2 = 0.53, r^2 UP_5 = 0.53; Fig. 2A), which means that the best match of sprawl and fragmentation patterns was detected at small extents, of just a few square kilometers. However, we found the opposite trend in the relation between the size of the reporting units and model performance of global models (best fitted to a linear function: r^2 *PUA* = 0.49, r^2 DIS_2 = 0.34, r^2 DIS_5 = 0.47; r^2 UP_2 = 0.49, r^2 UP_5 = 0.43; Fig. 2A), i.e., with model performance overall improving as extent increases, and peaking at coarse and intermediate extents. Likewise, we found a positive scaling trend when considering the whole set of local r^2 values from GWR models (instead of the final r^2 value) after organizing the models by type of configuration and hierarchical level (Fig. 2B). Indeed, the scaling trend became more pronounced, with higher hierarchical levels overall exhibiting higher model performance than lower hierarchical levels. Finally, the scale of urban sprawl measurement also affected the strength of the sprawl-fragmentation relationship. Models fitted with DIS_2 were overall more explicative and presented lower AICc values than those fitted with DIS_5, whereas UP_5-models performed better than UP_2-models (Fig. 2A,B; Table S3). However, in the multivariate models, some performed better with DIS_2 and others with DIS_5, and it also depended on the modeling approach.

Regarding the shape, the scale clearly affected the steepness and the intercept of the response (Fig. 2C,D), although in general the relationship between urban sprawl and landscape fragmentation is positive. This scale-effect was almost unaffected by the modeling technique. The intercept decreases as the level in the hierarchy increases within each type of configuration, independently of the urban sprawl metric considered and the *HP* (Fig. 2C). Although the spatial extent would seem to explain this behavior partially, when we order the intercepts by increasing extent some units do not fit well to the scaling trend (Fig. S15 to S17). The effect of the scale on the slope is more complex because it also depends on the urban sprawl metric and the type of configuration (Fig. 2D). According to the *DIS*-models, the slopes increased as the level in the hierarchy increased in all types of configuration, i.e., changes in urban sprawl suggest a stronger change in landscape



A)
B)
C)
D)
PUA-models
DIS2-models
DIS5-models
r2
mean size of the spatial extent (km2)
local r2
intercept
slope PUA-models
slope DIS-models
MUN
PRO
WAT
LAN
TYP
ASS
GR2
GR5
GR10
GR50
political
ecological
grid

Figure 2. Scale-effects on the strength and shape of the sprawl-fragmentation relationship. Results of the models performed with proportion of urban area (PUA) and degree of urban dispersion at 2 km (*DIS_2*) and at 5 km (*DIS_5*). (A) Scaling relationship between the median spatial extent of each reporting unit and model performance (r^2) of GWR models (logarithmic scaling curve; left graph) and global OLS models (linear scaling trend; right graph). (B) Box and whisker plots showing the distribution of local model performance (r^2) obtained through GWR modeling for each of the ten reporting units, which are grouped by type of configuration (political, ecological, and grid) and ordered from left to right by increasing hierarchical level and spatial extent: municipalities (MUN), provinces (PRO), watersheds (WAT), landscape units (LAN), landscape types (TYP), landscape associations (ASS), 2x2 km cells (GR2), 5x5 km cells (GR5), 10x10 km cells (GR10), 50x50 km cells (GR50). (C) Box and whisker plots showing the distribution of locally estimated intercepts for the reporting units. Units are Ln of effective number of meshes per 1000 km^2 * 1000 km^2 + 1. Filled circles indicate the intercepts estimated through global modeling. (D) Box and whisker plots showing the distribution of locally estimated slopes for the reporting units, according to PUA-models (left-axis) and DIS-models (right axis, units are m^2/UPU). Filled circles indicate the slopes estimated through global modeling.

fragmentation for the units at higher hierarchical level. This behavior was also observed in *PUA*- and *UP*-models for political and grid units, whereas we found the opposite behavior for ecological units, i.e., the slope decreases as the level in the hierarchy increases and the extent becomes larger. Watershed boundaries were not considered in this interpretation as they are not integrated in the hierarchy. Finally, the models fitted with DIS_2 presented steeper slopes than the models fitted with DIS_5.

Discussion

Can urban sprawl metrics predict landscape fragmentation consistently?

Our analysis demonstrates that anthropogenic landscape fragmentation is only partly explained by urban sprawl patterns. Overall, most of the variance in landscape fragmentation values (almost 80% on average) could not be explained by either the amount of urban areas (*PUA*) nor its dispersion (*DIS*) nor their combination (*UP* and multivariate models) in the global models. The widespread assumption of a high correlation between urban sprawl and landscape fragmentation patterns was not supported by our results. The sprawl-fragmentation relationship is more complex and non-stationary.

Although the local models explained on average almost two-thirds of the variability in landscape fragmentation, no single equation for any of the urban sprawl metrics, neither from OLS or GWR models, can predict landscape fragmentation consistently.

Much of the current confusion about the sprawl-fragmentation relationship arises from differences in how researchers conceptualize and quantify both urban sprawl and landscape fragmentation, as we highlighted in the Introduction. Land conversion into urban areas contributes necessarily to landscape fragmentation, since buildings constitute a barrier to species movement. Given that land can be used in many different spatial patterns, and some patterns represent a higher degree of landscape fragmentation than others (Fahrig 2003), metrics that consider the spatial arrangement of urban areas (e.g., *DIS*) should explain landscape fragmentation better than aspatial measures (Theobald et al. 1997; Lin and Fuller 2013; Bar-Massada et al. 2014). However, the differences in the explanatory power of *DIS* and *PUA* together vs. *PUA* alone were small. *PUA*-models presented on average a bit more explanatory power than *DIS*-models, though *DIS*-models were still better at some scales. In addition, *PUA*-models are insufficient to assess the sprawl-fragmentation relationship, since *PUA* – as well as housing density – is independent of its relative location to other urban areas (Jaeger et al. 2010b; Jaeger and Schwick 2014). Regarding *DIS*-models, we identified two conflicting points. First, an increase of *DIS* does not always imply an increase of landscape fragmentation. That strongly depends on the transport infrastructure, which might be built to get those increasingly dispersed urban areas better connected, or that might have facilitated the construction of new areas with a higher degree of dispersion. Second, the highest s_{eff}, which corresponds to the reporting unit being completely built-over, does not match with the highest value of *DIS*, which is reached when the buildings are located away (dispersed) from each other (but still inside the *HP*). This mismatch becomes evident in 'big cities and metropolitan areas' (one of the landscape associations), for which *PUA*- and *UP*-models provided a very high fit (ca. 85%), whereas *DIS*-models provided only a modest fit (ranging from 27.6 to 37.3%, depending on the *HP*).

We showed that combining both dimensions (amount of urban area and dispersion) through multivariate global regression improves model performance, whereas *UP* failed to explain notably more variation in seff than *PUA* alone. This may be due to the fact that *PUA* varied much more strongly than

DIS, so the variability in *UP* was more affected by *PUA* than by the smaller differences in *DIS*. Since many negative effects of urban sprawl are likely due to the scattered pattern of urban areas (e.g., the wildland-urban interface; Radeloff et al. 2005), *DIS* should always be included in monitoring systems of sustainable development to quantify the spatial dimension of 'urban sprawl'. Moreover, the *DIS* metric allowed us to analyze the effect of changing the scale of the urban sprawl analysis on the sprawl-fragmentation relationship.

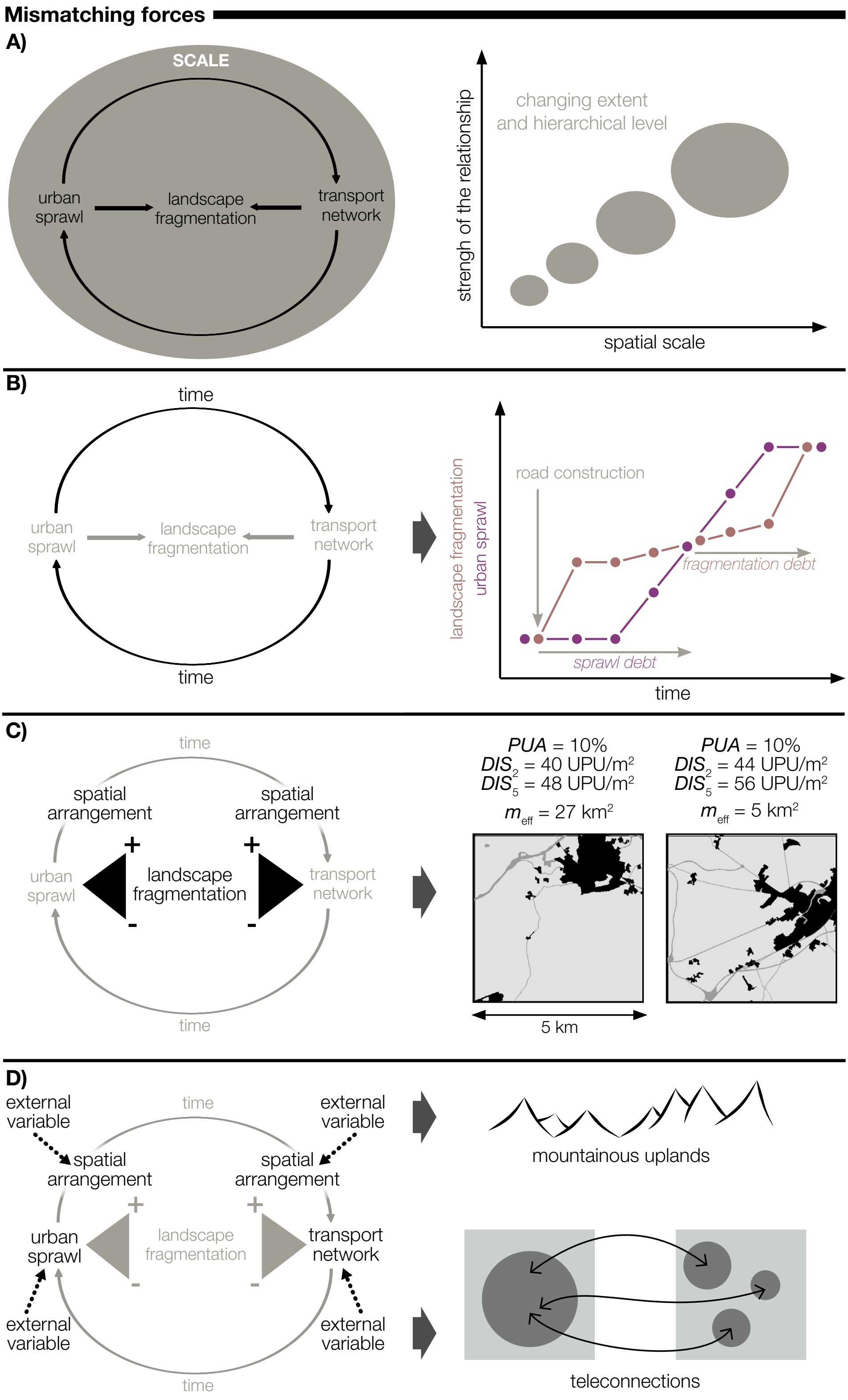
Need of an extended framework for the sprawl-fragmentation relationship

Our study highlights an important gap in the current state of knowledge about the landscape effects of urban sprawl. A central question is: Why is the sprawl-fragmentation relationship not as strong as expected? Here, by jointly conceptualizing landscape change and urban development processes, we propose four mechanisms that could explain the mismatch in the sprawl-fragmentation relationship (Fig. 3).

Scale dependency of the sprawl-fragmentation relationship

Our analysis confirmed that the sprawl-fragmentation relationship is scale-dependent. We revealed a substantial effect of changing the extent and the level in the hierarchy, though different modeling strategies produced differing scaling trends of model performance. The GWR models showed a decreasing scaling curve for extent, i.e., with sprawl and fragmentation patterns matching more closely at finer scales. This type of response has been found in previous studies that used various bandwidths of analysis to explore extent effects with GWR models (Bickford and Laffan 2006). As the extent decreases, the analysis becomes increasingly local and the model performance becomes increasingly inflated, which may obscure real differences in predictability between models (Jetz et al. 2005). Indeed, if instead we consider the whole range of local r^2 values as well as the model performance of global models, a growing scaling trend becomes evident, with increasing model performance as extent enlarges and the hierarchical level increases (Fig. 2A, B).

Untangling the forces that modulate this relationship is a challenge, since different forces may become relevant as scale changes (Wu et al. 2006). Fine scales reveal great spatial and temporal detail, but these details usually lose importance with coarsening scales because the information becomes averaged out in larger units (Fotheringham et al. 2002). Our results indicate that



Mismatching forces
A)
SCALE
urban sprawl
landscape fragmentation
transport network
changing extent and hierarchical level
strength of the relationship
spatial scale
B)
time
urban sprawl
landscape fragmentation
transport network
time
landscape fragmentation
urban sprawl
road construction
fragmentation debt
sprawl debt
time
C)
time
spatial arrangement
spatial arrangement
+
+
urban sprawl
landscape fragmentation
transport network
-
-
time
PUA = 10%
DIS_2 = 40 UPU/m²
DIS_5 = 48 UPU/m²
m_{eff} = 27 km²
PUA = 10%
DIS_2 = 44 UPU/m²
DIS_5 = 56 UPU/m²
m_{eff} = 5 km²
5 km
D)
external variable
time
external variable
spatial arrangement
spatial arrangement
+
+
urban sprawl
landscape fragmentation
transport network
-
-
external variable
time
external variable
mountainous uplands
teleconnections

Figure 3. Forces mismatching the sprawl-fragmentation relationship. (a) The feedback-loop model can be approached from a range of scales, but the strength of the sprawl-fragmentation relationship strongly varies with the extent and hierarchical level. (b) Influence of the temporal scale in the sprawl-fragmentation relationship. (c) Influence of the spatial arrangement of urban areas and transport infrastructures over the resulting landscape fragmentation. We show an example of two 5x5 km units with the same *PUA* and differing levels of *DIS* and landscape fragmentation (m_{eff}). (d) Additional variables might condition the spatial arrangement of development, e.g., a steep relief, as well as the magnitude of transport and urban development, e.g., urban land teleconnections.

in general the sprawl-fragmentation relationship is stronger at coarse extents and high hierarchical levels (Fig. 3A). Indeed, it is mainly at the smallest spatial extents where the proportion of the study area exhibiting negative slopes is largest (Fig. 2D; Fig. S2 to S7). Even for metropolitan areas, when they were examined separately (7 landscape units), we observed that local model performance varied from 3 to 80%. Therefore, we propose that it is at finer scales where the 'feedback loop model' fails more often, and where the modifying factors are more influential.

Time-lagged response of planning and development decisions

According to the feedback loop model, new transport infrastructure promotes the development of urban areas, whereas dispersed urban areas trigger demands for additional transport infrastructure, but they may do so with a significant time-lag (Bai 2007). At larger scales, the temporal correlation between sprawl and landscape fragmentation trends is commonly high (e.g., Irwin and Bockstael 2007; Su et al. 2012). However, a transient disequilibrium is likely to happen at finer scales between accessibility improvements and the development of new urban areas, with the latter progressively appearing over time and paying the '*sprawl debt*' (Fig. 3b). Similarly, the scattering of new urban areas would lead to transport network development, once a certain level of sprawl is reached and the road project is approved. Then, a changing spatial influence of transport infrastructure expansion on urban expansion and vice versa over time is expected, as Aljoufie et al. (2013) have found. Therefore, the delayed decision-making of urban and/or transport development would lead to spatial mismatches between sprawl patterns and expansion of transport infrastructures, followed by the subsequent landscape fragmentation. In the same way that time-lags in ecological communities can be managed to avoid paying the extinction debt through timely conservation measures (such as habitat restoration and landscape management; Kuussaari et al. 2009), the identification of these unpaid '*sprawl*' and '*fragmentation debts*' in terms of spatial mismatches implies that there is still a window of opportunity to prevent or improve future developments. In cases for which these mismatches between urban sprawl and landscape fragmentation are recognized, critical appraisal of the conservation and development plans is highly recommended for those areas to minimize the effects of new development in terms of sprawl (e.g., through clumped rather than dispersed development) or in terms of fragmentation (e.g., with alternative designs that protect roadless areas or defragmentation measures; van der Grift and Pouwels 2006; Selva et al. 2011).

Spatial arrangement of development

Much literature highlights the relevance of the spatial arrangement of urban development for their ecological effects (Sushinsky et al. 2013; Bar-Massada et al. 2014; Soga et al. 2014). However, our *DIS*-models were not able to explain landscape fragmentation patterns notably better than *PUA*-models. A key reason for this may be that we missed how the dispersed urban areas get connected to each other by roads. Overall, increasing urban sprawl carries development of transport infrastructure (Hawbaker et al. 2006), but the resulting landscape fragmentation will strongly depend on the relative location of the new transport links. We demonstrated that areas with high levels of *PUA* and/or *DIS* are accompanied by low to high levels of s_{eff} (Fig. 3C), i.e., sprawled patterns do not necessarily result in highly fragmented landscapes. This finding is encouraging, since it proves that certain spatial configurations of development can minimize some of the negative effects of urban sprawl. For example, infill development and the redevelopment of existing urban areas, e.g., land recycling at industrial sites, is a valuable strategy. Unfortunately, the amount of land in urban areas is probably insufficient to support the global future development needs (McMahon 2010), but are sufficient in most parts of Europe if they were actually used. Moreover, clustered development may or may not succeed in terms of achieving conservation objectives (Lenth et al. 2006; Pejchar et al. 2007), and the high cost of this land as well as political/regulatory obstacles to its development may lead many developers to avoid compact approaches on infill sites. Beyond the urban fringe, conservation development goes a step further by focusing on the preservation of land and the quality, quantity, and configuration of the resulting open space and on the linkages among open spaces within and outside the development boundary, while still keeping built-up areas clustered together (McMahon 2010). Thus, conservation development offers a valuable tool for meeting land preservation goals while reducing the risk of environmental hazards (e.g., flooding), erosion, infrastructure cost, and increasing property value (Pejchar et al. 2007). Finally, landscape connectivity can sometimes be partly restored by implementing defragmentation measures.

Teleconnections, topographic conditions, and other variables

The presence and the spatial arrangement of urban areas and transport infrastructure can be conditioned by additional variables (Fig. 3D). Some of the forces behind current patterns of development are the result of the strong legacy effect of early development patterns (Gonzalez-Abraham et al. 2007). In addition, transport network development in a given region is now increasingly influenced by distant drivers (Seto et al. 2012b). Such distant linkages or "teleconnections" between regions can determine the spatial arrangement of major transport corridors, which may attract new urban areas in their proximity (Zhang et al. 2013). For example, if a low-sprawled region is surrounded by highly sprawled regions, the first is prone to be fragmented by the development of major transport arteries between the surrounding regions. In addition, non-stationarity of the sprawl-fragmentation relationship indicates that spatial variables other than urban sprawl are affecting landscape fragmentation patterns. A steep relief is one of the recognized limiting factors for development (Peiyue et al. 2014). Our OLS models overestimated landscape fragmentation in mountainous areas, particularly at fine scales. The difference between flat and mountainous areas is twofold. On one hand, in mountainous areas, due to the difficulties of finding developable space, urban areas are much smaller and thus human population is more dispersed. On the other hand, a denser net of roads connects the urban settlements in flat areas, whereas in mountainous areas, all small urban areas are located along a few existing roads.

Conclusions

Our investigation revealed three characteristics of the sprawl-fragmentation relationship: it does not prevail, is non-stationary, and scale-dependent. Based on these characteristics, we expect the strength of the sprawl-fragmentation relationship to moderately vary among countries, as it varies for the reporting units throughout Spain. But the modifying mechanisms that we introduced above – namely, scale-effects, time-lags, spatial arrangements, and external variables – are likely operating everywhere, so mismatches are expected to occur more often than not. Therefore, contrary to previous expectations, urban sprawl is generally not a successful surrogate of landscape fragmentation, although its explanatory ability increases at coarser scales. Monitoring systems of sustainable development and other assessments should thus report on both with separate indicators, follow a multi-scale approach, and consider the continuous urban-rural gradient.

This study is the first to test explicitly the relationship between urban sprawl and landscape fragmentation patterns, and therefore is an important step towards a common understanding of the urban-landscape dynamics and a formulation of better planning strategies. We propose an extended framework for the sprawl-fragmentation relationship, in which we emphasize the linkages between urban sprawl, expansion of transport infrastructure, and landscape fragmentation (Fig. 3A to D). It integrates the main potential mechanisms that lead to spatial mismatches between urban sprawl and landscape fragmentation patterns, in particular at fine scales, along a continuum of urban sprawl. Although a rigorous attribution of relative magnitude to each of the modifying factors is not yet possible, this new perspective may help clarify current thinking in landscape ecology research and provides opportunities to test new hypotheses about leverage points for intervening in complex land-urban systems. This framework supports the fact that low levels of sprawl do not guarantee low levels of fragmentation as well as low levels of fragmentation do not guarantee compact development. However, the same applies to the high levels, which leaves open windows of opportunity for combating urban sprawl or landscape fragmentation, respectively, and mitigate their negative effects.

Most of the urban development expected to exist by 2030 on a global scale is not yet built (Seto et al. 2012a). Given the external costs of urban sprawl (about $400 billion per y. in the US due to increased capital investment needed for transportation infrastructure, among others factors; Whitmee et al. 2015) alternative patterns of development might generate great savings. Infill development will continue to be a critical goal for sustainable development, but for the developments expected to occur outside city centers the planners will need development strategies that minimize both sprawl and landscape fragmentation and protect key ecological assets. Conservation development embraces a broad range of techniques and strategies to advance specific development objectives, while concurrently acknowledging spatial heterogeneity and protecting networks of habitats and ecological flows (Pejchar et al. 2007). Through land-use planning, conservation development projects can harness development to protect and restore biodiversity, ecosystem services, and landscapes (Milder 2007) by modifying site selection and housing density, and promoting land stewardship (Pejchar et al. 2007).

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Supplementary material

Table S1. Description of the urban sprawl and landscape fragmentation geometries (land cover types).
Table S2. Description of the landscape fragmentation geometry (linear elements).
Table S3. Summary results for all OLS and GWR models.
Table S4. Parameter estimates from the univariate OLS and GWR models.
Table S5. Parameter estimates from the multivariate OLS and GWR models.
Table S6. Correlation analysis between urban sprawl metrics across scales.
Fig. S1. Study area and reporting units.
Fig. S2 to S14. Mapped local r^2 values, slopes, and residuals from *PUA*-, *DIS*-, *UP*-models, and multivariate models.
Fig. S15 to S17. Parameter estimates ordered by spatial extent of the reporting units.

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Table S2. Attribution of the linear fragmenting elements to the fragmentation geometry.

Element	Included in F.G.[a]	Buffer (m)
Highway	Yes	15
Major road	Yes	10
Secondary road	Yes	6
Local connecting road	Yes	5
Track	No	-
Trail	No	-
High-speed railway	Yes	4
Conventional railway	Yes	2

[a] Fragmentation geometry

Table S3. Attribution of the linear fragmenting elements to the fragmentation geometry.

Table S3. Summary results for all the ordinary least square (OLS) regression models and geographically weighted regression (GWR) models. The values of Moran's Index are also reported.

Scale	Type of reporting unit	Model	Model approach	r^2	sigma	AICc	ΔAICc	Moran's I
Political	*Provinces*	$\mathrm{Ln}(S_{eff}) \sim DIS_2$	OLS	0.09	0.750	124.40	6.833	**0.409**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	OLS	0.13	0.714	122.08	4.514	**0.350**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	OLS	0.21	0.651	117.73	0.163	**0.466**
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	OLS	0.21	0.654	117.91	0.344	**0.464**
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	OLS	0.21	0.649	117.57	0.000	**0.461**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	OLS	0.21	0.665	120.07	2.506	**0.468**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	OLS	0.22	0.655	119.35	1.779	**0.436**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2$	GWR	0.48	0.74	118.88	13.20	0.098
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	GWR	0.25	0.82	120.45	14.77	**0.246**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	GWR	0.62	0.64	105.68	0.00	0.124
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	GWR	0.62	0.64	105.98	0.30	0.120
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	GWR	0.62	0.64	106.08	0.40	0.123
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	GWR	n.a.	n.a.	n.a.	n.a.	n.a.
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	GWR	n.a.	n.a.	n.a.	n.a.	n.a.
	Municipalities	$\mathrm{Ln}(S_{eff}) \sim DIS_2$	OLS	0.11	1.651	26522.43	2035.674	**0.547**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	OLS	0.10	1.658	26557.84	2071.084	**0.565**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	OLS	0.26	1.378	25086.12	599.368	**0.488**
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	OLS	0.25	1.385	25130.54	643.782	**0.492**
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	OLS	0.26	1.366	25018.85	532.094	**0.489**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	OLS	0.27	1.352	24937.47	450.711	**0.480**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	OLS	0.31	1.277	24486.76	0.000	**0.448**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2$	GWR	0.58	0.90	21013.77	5844.01	**0.235**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	GWR	0.48	0.99	22436.78	7267.02	**0.354**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	GWR	0.89	0.56	15324.90	155.14	-0.002
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	GWR	0.89	0.56	15302.09	132.33	-0.002
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	GWR	0.89	0.55	15169.76	0.00	-0.004
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	GWR	0.61	0.86	20243.95	5074.19	**0270**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	GWR	0.59	0.88	20574.25	5404.49	**0.291**
Ecological	*Landscape Associations*	$\mathrm{Ln}(S_{eff}) \sim DIS_2$	OLS	0.36	0.808	65.55	0.000	0.186
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	OLS	0.24	0.961	69.52	3.970	**0.274**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	OLS	0.30	0.885	67.62	2.070	0.084
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	OLS	0.29	0.893	67.85	2.299	0.085
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	OLS	0.30	0.889	67.74	2.193	0.084
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	OLS	0.43	0.760	65.98	0.430	0.082
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	OLS	0.36	0.854	68.64	3.090	0.087
		$\mathrm{Ln}(S_{eff}) \sim DIS_2$	GWR	0.50	0.85	65.26	1.23	0.209
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	GWR	0.43	0.92	69.88	5.85	**0.295**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	GWR	0.81	0.62	64.21	0.18	0.082
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	GWR	0.81	0.62	64.26	0.23	0.076
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	GWR	0.81	0.62	64.03	0.00	0.075
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	GWR	n.a.	n.a.	n.a.	n.a.	n.a.
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	GWR	n.a.	n.a.	n.a.	n.a.	n.a.
	Landscape Types	$\mathrm{Ln}(S_{eff}) \sim DIS_2$	OLS	0.29	0.975	268.64	1.659	**0.497**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	OLS	0.25	1.035	274.20	7.212	**0.443**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	OLS	0.19	1.114	281.17	14.184	**0.467**
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	OLS	0.18	1.126	282.19	15.211	**0.465**
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	OLS	0.18	1.123	281.93	14.949	**0.463**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	OLS	0.32	0.946	266.98	0.000	**0.485**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	OLS	0.31	0.956	267.92	0.935	**0.436**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2$	GWR	0.69	0.74	233.09	0.00	0.038
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	GWR	0.42	0.93	260.55	27.46	**0.329**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	GWR	0.57	0.84	249.44	16.35	**0.151**
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	GWR	0.57	0.85	250.68	17.59	**0.149**
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	GWR	0.57	0.84	249.71	16.62	**0.147**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	GWR	0.70	0.74	234.65	1.56	0.099
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	GWR	0.47	0.88	252.18	19.09	**0.359**

Scale	Type of reporting unit	Model	Model approach	r^2	sigma	AICc	ΔAICc	Moran's I
	Landscape Units	$\mathrm{Ln}(S_{eff}) \sim DIS_2$	OLS	0.20	1.287	3508.06	70.30	**0.536**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	OLS	0.13	1.400	3603.82	166.06	**0.569**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	OLS	0.17	1.338	3552.37	114.61	**0.605**
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	OLS	0.16	1.355	3566.41	128.65	**0.606**
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	OLS	0.16	1.346	3559.30	121.54	**0.605**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	OLS	0.25	1.208	3437.76	0.00	**0.563**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	OLS	0.23	1.240	3467.56	29.80	**0.581**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2$	GWR	0.64	0.810	2807.76	227.57	**0.140**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	GWR	0.50	0.930	3090.95	510.76	**0.273**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	GWR	0.78	0.688	2584.39	4.20	0.020
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	GWR	0.80	0.678	2590.92	10.73	0.002
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	GWR	0.80	0.675	2580.19	0.00	0.001
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	GWR	0.64	0.804	2795.31	215.12	0.191
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	GWR	0.58	0.858	2920.02	339.83	**0.263**
	Watersheds	$\mathrm{Ln}(S_{eff}) \sim DIS_2$	OLS	0.09	1.488	385.96	27.742	**0.228**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	OLS	0.11	1.453	383.17	24.951	**0.206**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	OLS	0.25	1.225	363.00	4.783	**0.305**
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	OLS	0.25	1.231	363.60	5.383	**0.304**
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	OLS	0.27	1.199	360.45	2.228	**0.301**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	OLS	0.26	1.217	363.33	5.115	**0.294**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	OLS	0.30	1.165	358.22	0.000	**0.267**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2$	GWR	0.42	1.04	356.05	26.81	0.015
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	GWR	0.36	1.08	364.54	35.30	0.035
		$\mathrm{Ln}(S_{eff}) \sim PUA$	GWR	0.66	0.86	329.45	0.21	-0.021
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	GWR	0.65	0.86	330.75	1.51	-0.020
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	GWR	0.66	0.86	329.24	0.00	-0.020
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	GWR	0.51	0.94	333.00	3.76	0.059
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	GWR	0.51	0.94	333.78	4.54	**0.074**
Grid	*50x50 km cells*	$\mathrm{Ln}(S_{eff}) \sim DIS_2$	OLS	0.12	0.834	527.44	11.10	**0.576**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	OLS	0.11	0.841	529.14	12.80	**0.548**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	OLS	0.16	0.800	519.29	2.95	**0.556**
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	OLS	0.15	0.809	521.34	5.00	**0.555**
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	OLS	0.15	0.804	520.22	3.88	**0.553**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	OLS	0.17	0.791	518.03	1.69	**0.573**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	OLS	0.18	0.784	516.34	0.00	**0.554**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2$	GWR	0.74	0.586	391.66	1.83	**0.141**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	GWR	0.36	0.812	489.30	99.47	**0.427**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	GWR	0.83	0.524	389.83	0.00	0.054
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	GWR	0.82	0.530	394.42	4.59	0.058
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	GWR	0.82	0.527	392.02	2.19	0.058
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	GWR	0.58	0.693	441.03	51.20	**0.340**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	GWR	0.36	0.804	483.74	93.91	**0.468**
	10x10 km cells	$\mathrm{Ln}(S_{eff}) \sim DIS_2$	OLS	0.17	1.319	15342.50	355.29	**0.693**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	OLS	0.10	1.426	15725.49	738.28	**0.713**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	OLS	0.16	1.339	15415.59	428.38	**0.766**
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	OLS	0.15	1.355	15473.99	486.78	**0.768**
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	OLS	0.15	1.346	15440.68	453.47	**0.768**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	OLS	0.23	1.227	14987.21	0.00	**0.720**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	OLS	0.21	1.252	15085.18	97.97	**0.729**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2$	GWR	0.62	0.79	11777.47	3033.69	**0.449**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	GWR	0.52	0.89	12861.43	4117.65	**0.536**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	GWR	0.91	0.49	8852.60	108.82	0.017
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	GWR	0.91	0.49	8787.60	43.82	**0.022**
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	GWR	0.91	0.49	8743.78	0.00	0.019
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	GWR	0.62	0.79	11805.00	3061.22	**0.498**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	GWR	0.59	0.82	12147.09	3403.31	**0.537**

Scale	Type of reporting unit	Model	Model approach	r^2	sigma	AICc	ΔAICc	Moran's I
	5x5 km cells	$\mathrm{Ln}(S_{eff}) \sim DIS_2$	OLS	0.17	1.536	63898.04	1600.62	**0.737**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	OLS	0.12	1.626	65023.58	2726.16	**0.757**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	OLS	0.15	1.565	64275.90	1978.48	**0.816**
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	OLS	0.15	1.579	64440.21	2142.79	**0.820**
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	OLS	0.15	1.562	64238.67	1941.25	**0.822**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	OLS	0.23	1.415	62297.42	0.00	**0.757**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	OLS	0.23	1.425	62433.33	135.91	**0.764**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2$	GWR	0.69	0.77	45810.01	13660.33	**0.497**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	GWR	0.59	0.88	50520.95	18371.27	**0.584**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	GWR	0.89	0.51	32349.65	199.97	**0.202**
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	GWR	0.89	0.51	32163.08	13.40	**0.205**
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	GWR	0.89	0.51	32149.68	0.00	**0.199**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	GWR	0.68	0.78	46293.03	14143.35	**0.546**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	GWR	0.60	0.86	49882.60	17732.92	**0.609**
	2x2 km cells	$\mathrm{Ln}(S_{eff}) \sim DIS_2$	OLS	0.15	1.911	425603.97	10069.45	**0.810**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	OLS	0.12	1.981	429980.99	14446.47	**0.811**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	OLS	0.15	1.909	425515.64	9981.12	**0.866**
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	OLS	0.15	1.905	425213.57	9679.05	**0.873**
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	OLS	0.16	1.888	424119.47	8584.95	**0.869**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	OLS	0.22	1.760	415534.52	0.00	**0.825**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	OLS	0.21	1.779	416891.66	1357.14	**0.817**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2$	GWR	0.72	0.80	293932.09	41239.73	**0.613**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5$	GWR	0.71	0.81	297468.19	44775.83	**0.626**
		$\mathrm{Ln}(S_{eff}) \sim PUA$	GWR	0.80	0.68	253612.89	920.53	**0.569**
		$\mathrm{Ln}(S_{eff}) \sim UP_2$	GWR	0.81	0.67	252692.36	0.00	**0.572**
		$\mathrm{Ln}(S_{eff}) \sim UP_5$	GWR	0.81	0.68	253253.50	561.14	**0.564**
		$\mathrm{Ln}(S_{eff}) \sim DIS_2 + PUA$	GWR	0.75	0.76	282695.13	30002.77	**0.622**
		$\mathrm{Ln}(S_{eff}) \sim DIS_5 + PUA$	GWR	0.74	0.77	285751.06	33058.70	**0.623**

$\mathrm{Ln}(S_{eff})$. Ln (effective mesh size per 1000 km^2 * 1000km^2 + 1)
DIS = degree of urban dispersion
PUA = proportion of urban area
UP = degree of urban permeation
$_{2,5}$ subscripts indicate the horizon of perception for which *DIS* and then *UP* were calculated (2 km or 5 km respectively)

Table S4. Parameter estimates from univariate OLS and GWR models, for the relationship between landscape fragmentation (effective mesh density; S_{eff}) and urban sprawl metrics (*DIS*, *PUA* and *UP*). Subscripts 2 and 5 indicate the horizon of perception for which urban sprawl metric was calculated (2 km or 5 km, respectively). For the GWR models, the median local coefficients are shown. Ln(S_{eff}) = Ln (effective mesh size per 1000 km^2 * 1000km^2 + 1). β_1 units are in m^2/UPU for *DIS*-models, and km^2/UPU for *UP*-models.

Model	Type of reporting unit	β_0 OLS	β_0 GWR	sd β_0 OLS	sd β_0 GWR	β_1 OLS	β_1 GWR	sd β_1 OLS	sd β_1 GWR
$Ln(S_{eff}) \sim DIS_2$	*Provinces*	5.791	6.044	1.212	1.873	0.064	0.059	0.030	0.047
	Municipalities	7.813	8.291	0.046	0.318	0.043	0.023	0.001	0.010
	Landscape associations	2.901	3.872	1.510	1.673	0.134	0.112	0.039	0.043
	Landscape types	4.159	4.445	0.688	1.369	0.112	0.106	0.018	0.037
	Landscape units	6.382	6.752	0.135	0.588	0.067	0.052	0.004	0.018
	Watersheds	6.138	6.884	0.821	1.639	0.069	0.042	0.020	0.040
	Grid 50x50 km cells	6.282	6.127	0.407	1.127	0.058	0.055	0.011	0.031
	Grid 10x10 km cells	7.275	7.522	0.047	0.234	0.047	0.033	0.001	0.008
	Grid 5x5 km cells	9.361	9.713	0.015	0.136	0.034	0.017	0.001	0.005
	Grid 2x2 km cells	11.681	12.003	0.005	0.070	0.031	0.010	0.000	0.004
$Ln(S_{eff}) \sim DIS_5$	*Provinces*	5.076	5.973	1.241	1.397	0.050	0.036	0.019	0.021
	Municipalities	7.293	7.798	0.064	0.371	0.029	0.020	0.001	0.006
	Landscape associations	2.417	3.753	2.198	2.600	0.088	0.070	0.034	0.040
	Landscape types	3.782	4.261	0.836	1.272	0.072	0.067	0.013	0.020
	Landscape units	6.452	6.608	0.168	0.651	0.036	0.033	0.003	0.011
	Watersheds	5.796	5.834	0.821	1.671	0.047	0.040	0.012	0.025
	Grid 50x50 km cells	6.272	6.851	0.424	0.820	0.035	0.026	0.007	0.014
	Grid 10x10 km cells	7.440	7.567	0.054	0.224	0.022	0.017	0.001	0.004
	Grid 5x5 km cells	9.401	9.716	0.017	0.116	0.015	0.009	0.000	0.002
	Grid 2x2 km cells	11.701	12.022	0.005	0.072	0.015	0.004	0.000	0.002
$Ln(S_{eff}) \sim PUA$	*Provinces*	7.914	7.887	0.167	0.242	0.191	0.193	0.055	0.077
	Municipalities	8.894	9.041	0.014	0.268	0.095	0.091	0.002	0.188
	Landscape associations	7.813	7.693	0.213	0.319	0.073	0.057	0.024	0.046
	Landscape types	8.073	7.954	0.122	0.236	0.105	0.148	0.023	0.054
	Landscape units	8.361	8.380	0.038	0.236	0.111	0.187	0.007	0.103
	Watersheds	8.588	8.562	0.116	0.335	0.073	0.087	0.012	0.047
	Grid 50x50 km cells	8.097	8.027	0.078	0.278	0.172	0.261	0.028	0.159
	Grid 10x10 km cells	8.476	8.558	0.018	0.239	0.122	0.151	0.004	0.230
	Grid 5x5 km cells	9.974	10.127	0.009	0.154	0.109	0.083	0.002	0.121
	Grid 2x2 km cells	11.935	12.108	0.004	0.074	0.093	0.048	0.001	0.032
$Ln(S_{eff}) \sim UP_2$	*Provinces*	7.950	7.954	0.160	0.234	0.408	0.416	0.119	0.167
	Municipalities	8.921	9.072	0.014	0.247	0.201	0.200	0.004	0.459
	Landscape associations	7.830	7.757	0.212	0.311	0.151	0.118	0.051	0.096
	Landscape types	8.100	7.987	0.121	0.233	0.216	0.312	0.048	0.116
	Landscape units	8.390	8.414	0.037	0.244	0.231	0.415	0.016	0.283
	Watersheds	8.615	8.580	0.115	0.329	0.150	0.182	0.024	0.101
	Grid 50x50 km cells	8.132	8.101	0.076	0.261	0.359	0.539	0.062	0.347
	Grid 10x10 km cells	8.505	8.589	0.018	0.225	0.250	0.343	0.009	0.561
	Grid 5x5 km cells	9.997	10.139	0.009	0.149	0.226	0.200	0.004	0.322
	Grid 2x2 km cells	11.947	12.108	0.004	0.073	0.205	0.132	0.001	0.089
$Ln(S_{eff}) \sim UP_5$	*Provinces*	7.940	7.916	0.161	0.233	0.258	0.259	0.074	0.104
	Municipalities	8.902	9.006	0.014	0.265	0.130	0.149	0.002	0.301
	Landscape associations	7.827	7.735	0.212	0.313	0.096	0.075	0.032	0.060
	Landscape types	8.093	7.965	0.121	0.231	0.138	0.198	0.031	0.074
	Landscape units	8.380	8.390	0.037	0.248	0.149	0.283	0.010	0.176
	Watersheds	8.593	8.571	0.114	0.329	0.101	0.114	0.016	0.062
	Grid 50x50 km cells	8.124	8.093	0.076	0.262	0.228	0.332	0.038	0.215
	Grid 10x10 km cells	8.497	8.555	0.018	0.236	0.161	0.247	0.005	0.379
	Grid 5x5 km cells	9.985	10.115	0.009	0.155	0.150	0.151	0.003	0.229
	Grid 2x2 km cells	11.935	12.101	0.004	0.074	0.137	0.093	0.001	0.062

Table S5. Parameter estimates from multivariate OLS and GWR models, for the relationship between landscape fragmentation (effective mesh density; S_{eff}) and urban sprawl metrics (*DIS*, *PUA* and *UP*). Subscripts 2 and 5 indicate the horizon of perception for which urban sprawl metric was calculated (2 km or 5 km, respectively). For the GWR models, the median local coefficients are shown. We did not perform multiple GWR models for provinces and landscape associations (n.a. = "not available") because of the small sample size of these reporting units. Ln(S_{eff}) = Ln (effective mesh size per 1000 km^2 * 1000km^2 + 1). β_1 units are in m^2/UPU for *DIS*-models, and km^2/UPU and β_2 units are in %.

Model	Type of reporting unit	β_0 OLS	β_0 GWR	sd β_0 OLS	sd β_0 GWR	β_1 OLS	β_1 GWR	sd β_1 OLS	sd β_1 GWR	β_2 OLS	β_2 GWR	sd β_2 OLS	sd β_2 GWR
Ln(S_{eff}) ~ DIS_2 + PUA	*Provinces*	8.238	n.a.	1.479	n.a.	-0.009	n.a.	0.040	n.a.	0.203	n.a.	0.078	n.a.
	Municipalities	8.380	8.625	0.044	0.241	0.017	0.009	0.001	0.008	0.085	0.084	0.002	0.018
	Landscape associations	4.242	n.a.	1.709	n.a.	0.095	n.a.	0.045	n.a.	0.042	n.a.	0.027	n.a.
	Landscape types	4.887	6.156	0.774	1.429	0.089	0.058	0.021	0.041	0.048	0.070	0.025	0.060
	Landscape units	6.844	7.342	0.142	0.537	0.048	0.033	0.004	0.017	0.069	0.090	0.008	0.034
	Watersheds	7.545	8.330	0.790	1.045	0.026	0.002	0.020	0.027	0.066	0.075	0.013	0.026
	Grid 50x50 km cells	7.227	7.199	0.484	1.019	0.026	0.032	0.014	0.031	0.127	0.104	0.037	0.088
	Grid 10x10 km cells	7.540	7.803	0.047	0.205	0.034	0.023	0.002	0.007	0.082	0.091	0.004	0.028
	Grid 5x5 km cells	9.435	9.763	0.015	0.110	0.026	0.013	0.001	0.005	0.077	0.071	0.002	0.028
	Grid 2x2 km cells	11.688	11.997	0.005	0.065	0.022	0.008	0.000	0.004	0.067	0.038	0.001	0.023
Ln(S_{eff}) ~ DIS_5 + PUA	*Provinces*	6.726	n.a.	1.396	n.a.	0.019	n.a.	0.022	n.a.	0.156	n.a.	0.069	n.a.
	Municipalities	7.532	7.714	0.056	0.293	0.022	0.019	0.001	0.004	0.087	0.089	0.002	0.014
	Landscape associations	4.663	n.a.	2.384	n.a.	0.050	n.a.	0.038	n.a.	0.054	n.a.	0.028	n.a.
	Landscape types	4.652	5.527	0.856	1.063	0.056	0.042	0.014	0.017	0.067	0.061	0.023	0.025
	Landscape units	6.867	7.029	0.162	0.590	0.026	0.022	0.003	0.010	0.090	0.112	0.007	0.025
	Watersheds	6.631	6.833	0.751	1.007	0.030	0.023	0.011	0.016	0.065	0.079	0.012	0.024
	Grid 50x50 km cells	7.083	7.794	0.459	0.661	0.018	0.006	0.008	0.012	0.131	0.147	0.034	0.046
	Grid 10x10 km cells	7.580	7.747	0.051	0.203	0.016	0.013	0.001	0.004	0.104	0.122	0.004	0.022
	Grid 5x5 km cells	9.390	9.637	0.016	0.087	0.012	0.008	0.000	0.002	0.094	0.095	0.002	0.016
	Grid 2x2 km cells	11.687	12.000	0.005	0.065	0.011	0.003	0.000	0.002	0.075	0.044	0.001	0.021

Table S6. Correlations (Spearman's rank correlation) between urban sprawl variables (*proportion of urban area* = *PUA*; *degree of urban permeation* = *UP*; *degree of urban dispersion* = *DIS*) for all reporting units and differing horizons of perception (*HP*) across Spain. All the correlations were significant at $P < 0.005$.

	PUA		*UP*	
	HP = 2 km	*HP* = 5 km	*HP* = 2 km	*HP* = 5 km
Provinces				
DIS	0.920	0.830	0.940	0.860
PUA	-	-	0.997	0.996
Municipalities				
DIS	0.727	0.241	0.826	0.391
PUA	-	-	0.985	0.982
Landscape associations				
DIS	0.940	0.734	0.948	0.792
PUA	-	-	0.998	0.991
Landscape types				
DIS	0.924	0.680	0.941	0.737
PUA	-	-	0.998	0.995
Landscape units				
DIS	0.833	0.443	0.874	0.532
PUA	-	-	0.996	0.993
Watersheds				
DIS	0.852	0.625	0.868	0.665
PUA	-	-	0.999	0.997
Grid 50x50 km units				
DIS	0.888	0.750	0.920	0.810
PUA	-	-	0.996	0.994
Grid 10x10 km units				
DIS	0.805	0.340	0.861	0.463
PUA	-	-	0.994	0.987
Grid 5x5 km units				
DIS	0.805	0.492	0.862	0.563
PUA	-	-	0.993	0.991
Grid 2x2 km units				
DIS	0.946	0.917	0.961	0.926
PUA	-	-	0.998	0.999

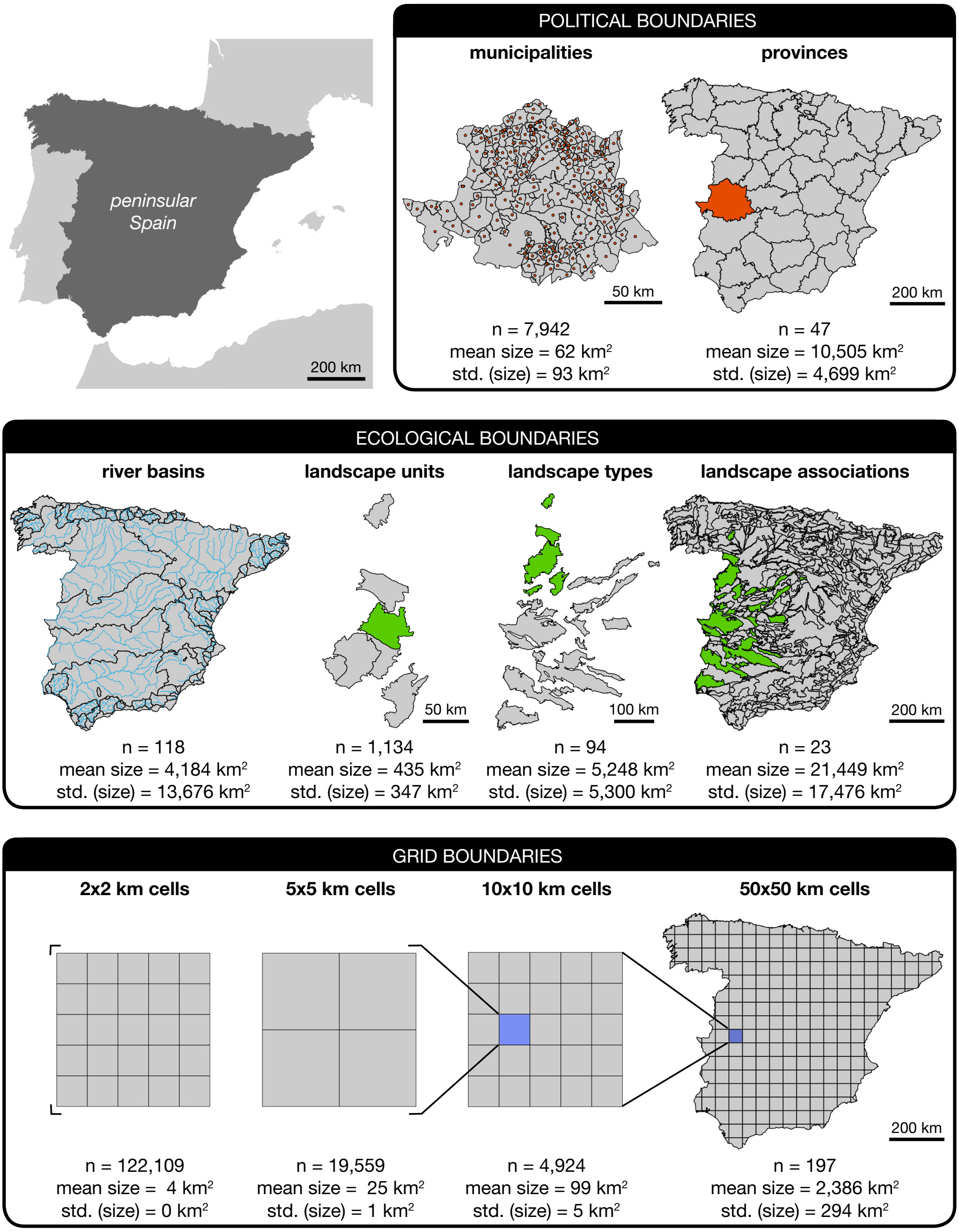


Figure S1. Study area and political, ecological, and grid boundaries used as planning units for which landscape fragmentation and urban sprawl were reported, and then analyzed.

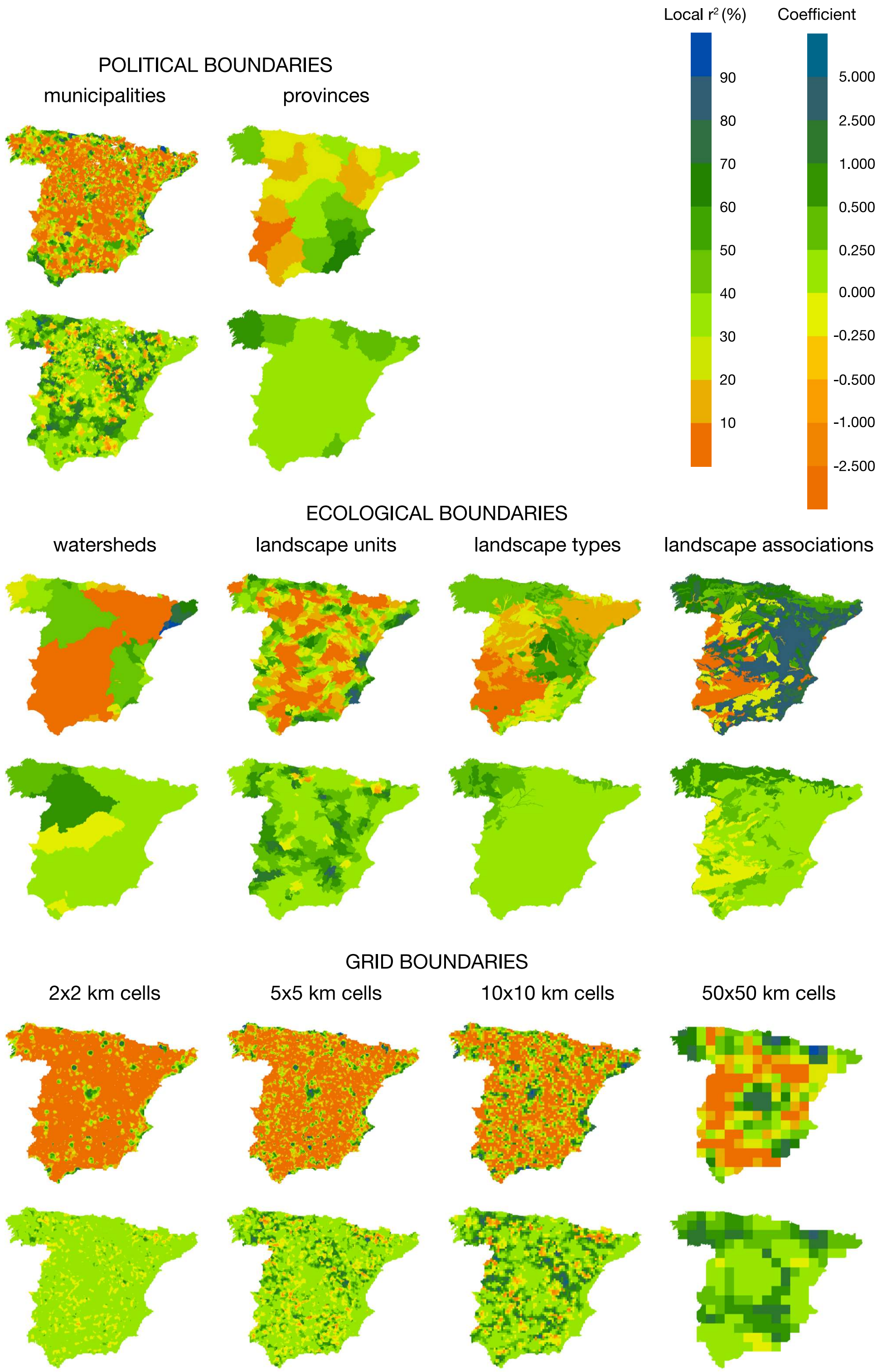


Figure S2. Mapped local r^2 values (up) and local slopes (down) from *PUA*-models.

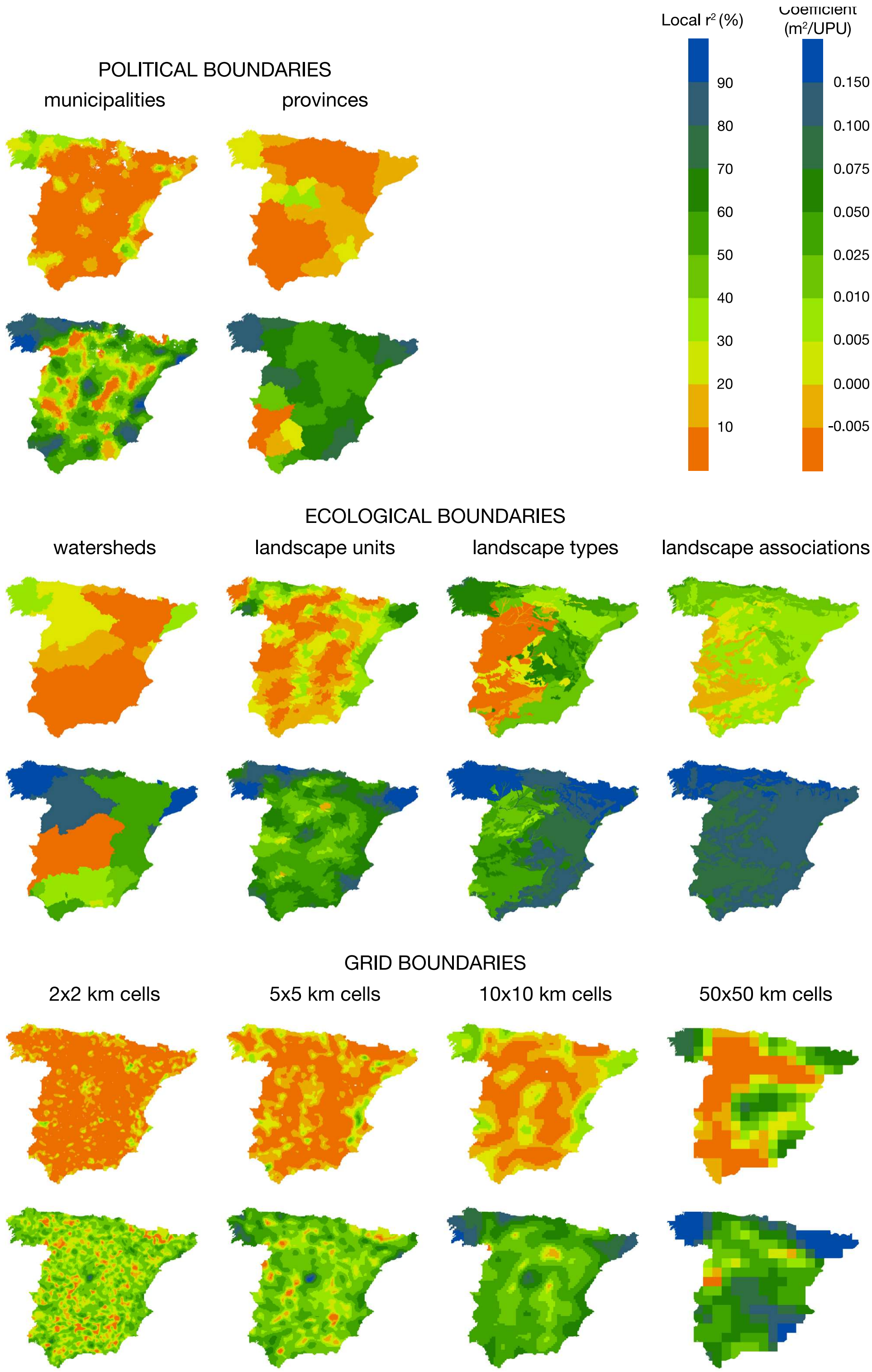


Figure S3. Mapped local r^2 values (up) and local slopes (down) from DIS_2-models.

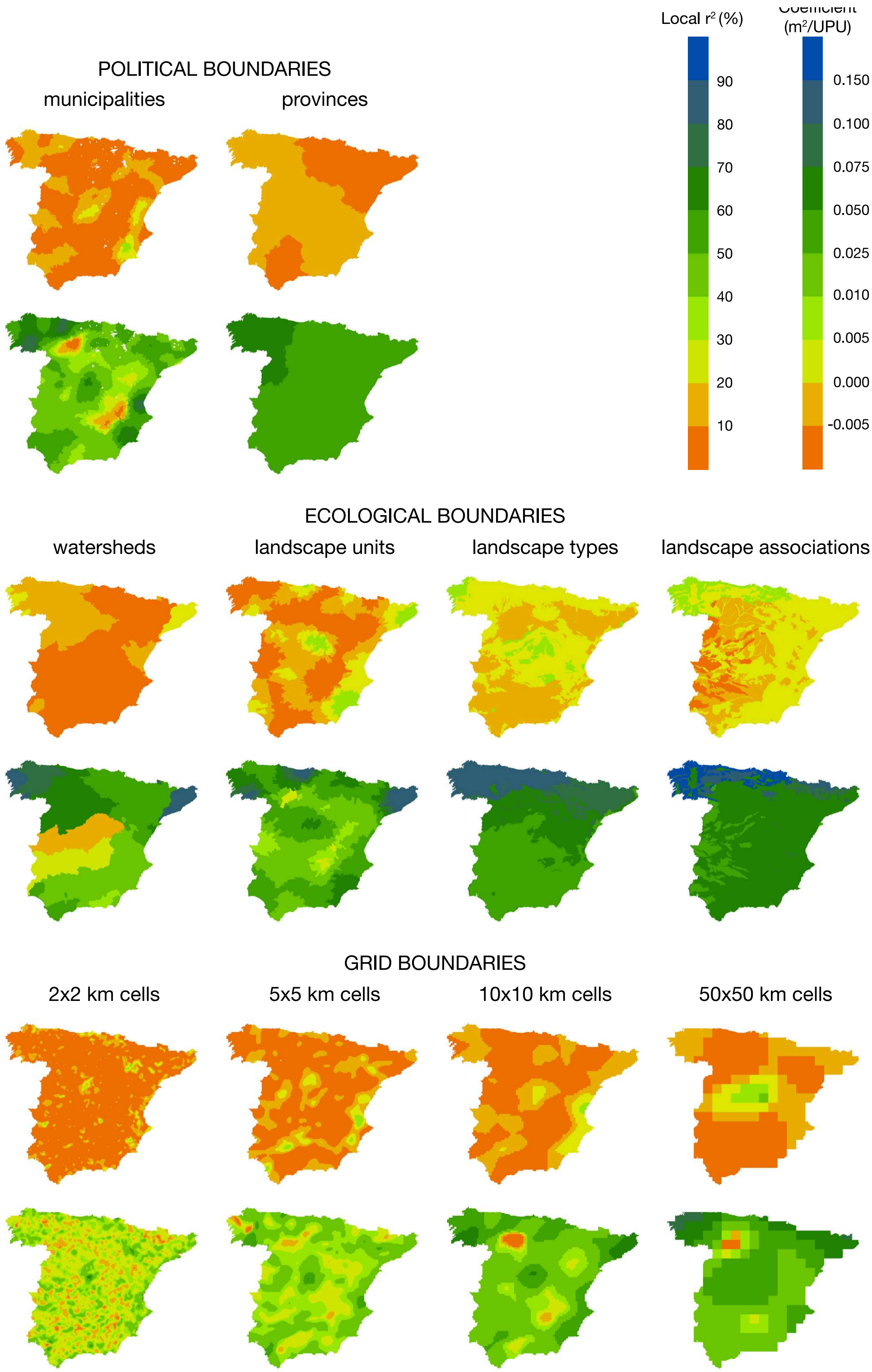


Figure S4. Mapped local r^2 values (up) and local slopes (down) from *DIS*-models.

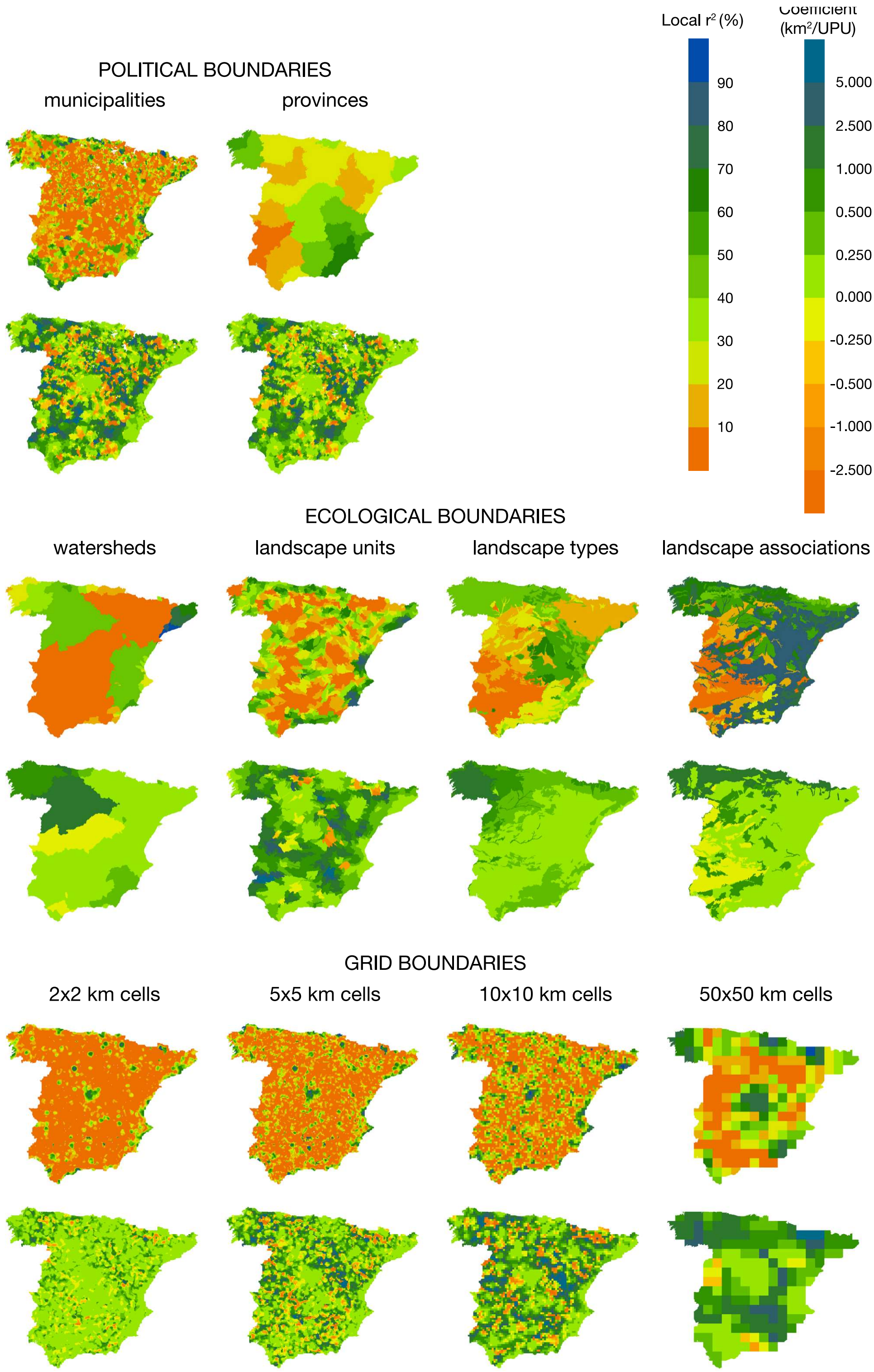


Figure S5. Mapped local r² values (up) and local slopes (down) from UP_2-models.

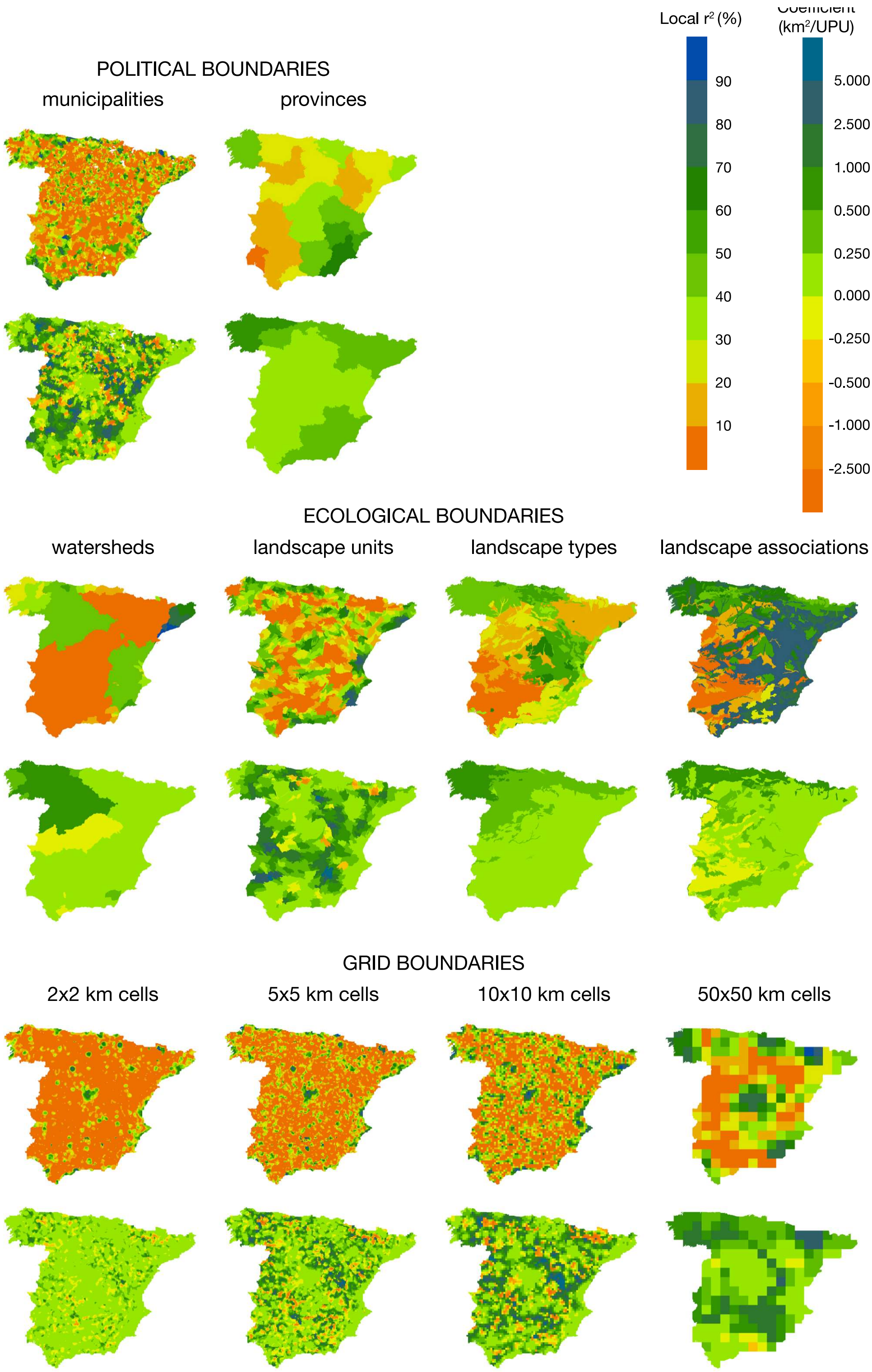


Figure S6. Mapped local r² values (up) and local slopes (down) from *UP*-models.

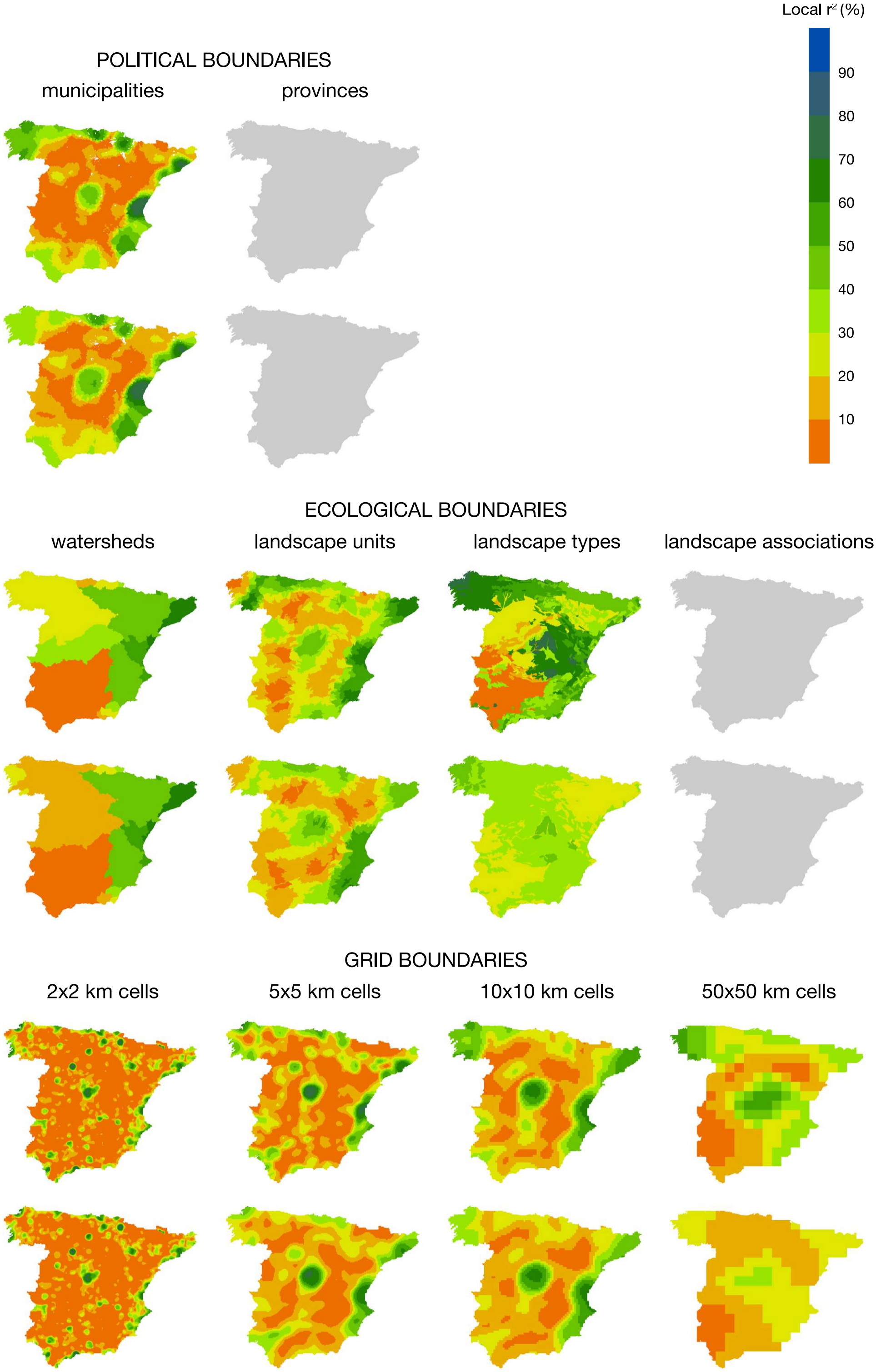


Figure S7. Mapped local r^2 values from multivariate models with *PUA* and DIS_2 (up) or DIS_5 (down).

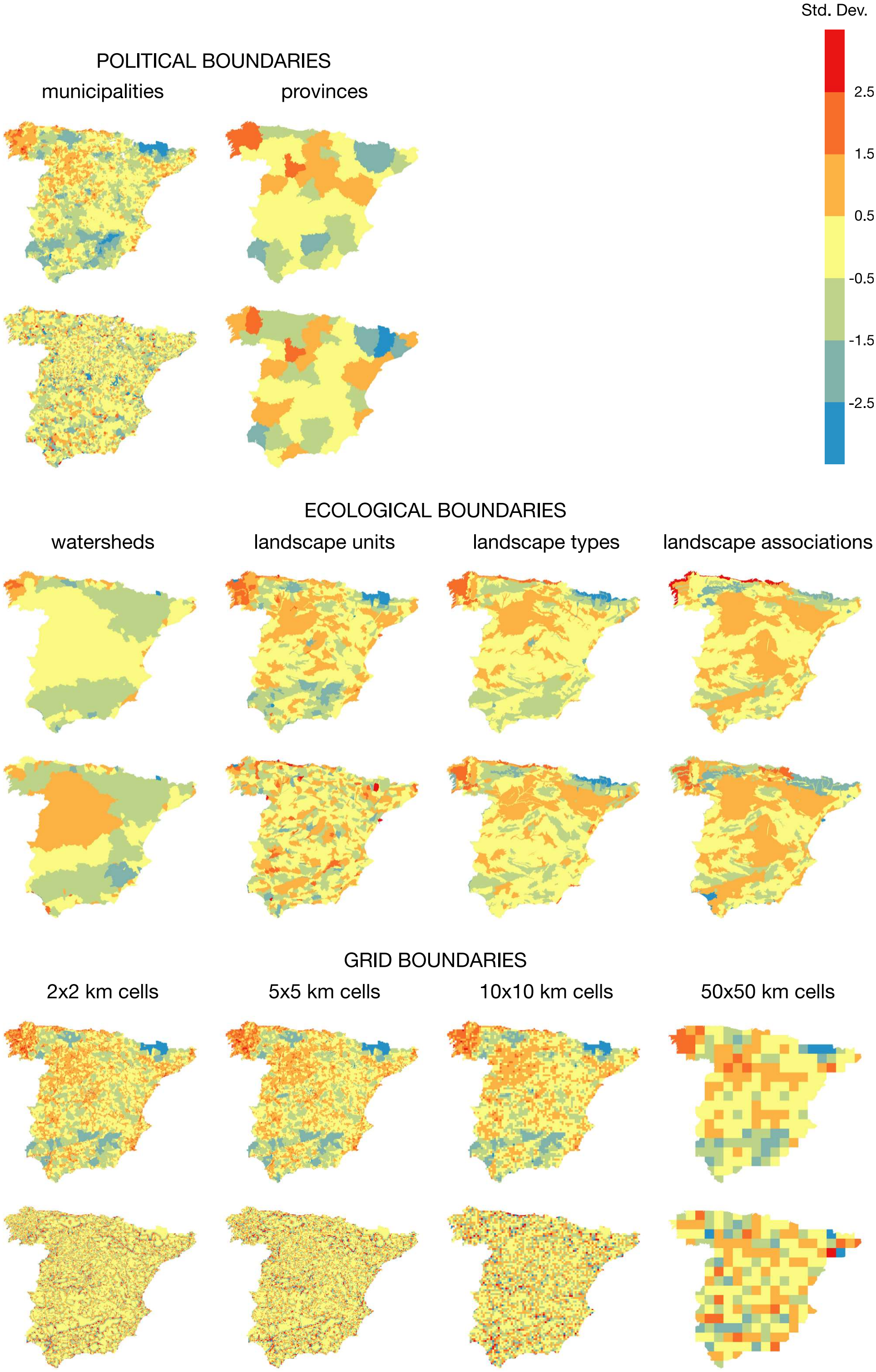


Figure S8. Mapped global (up) and local (down) residuals from *PUA*-models.

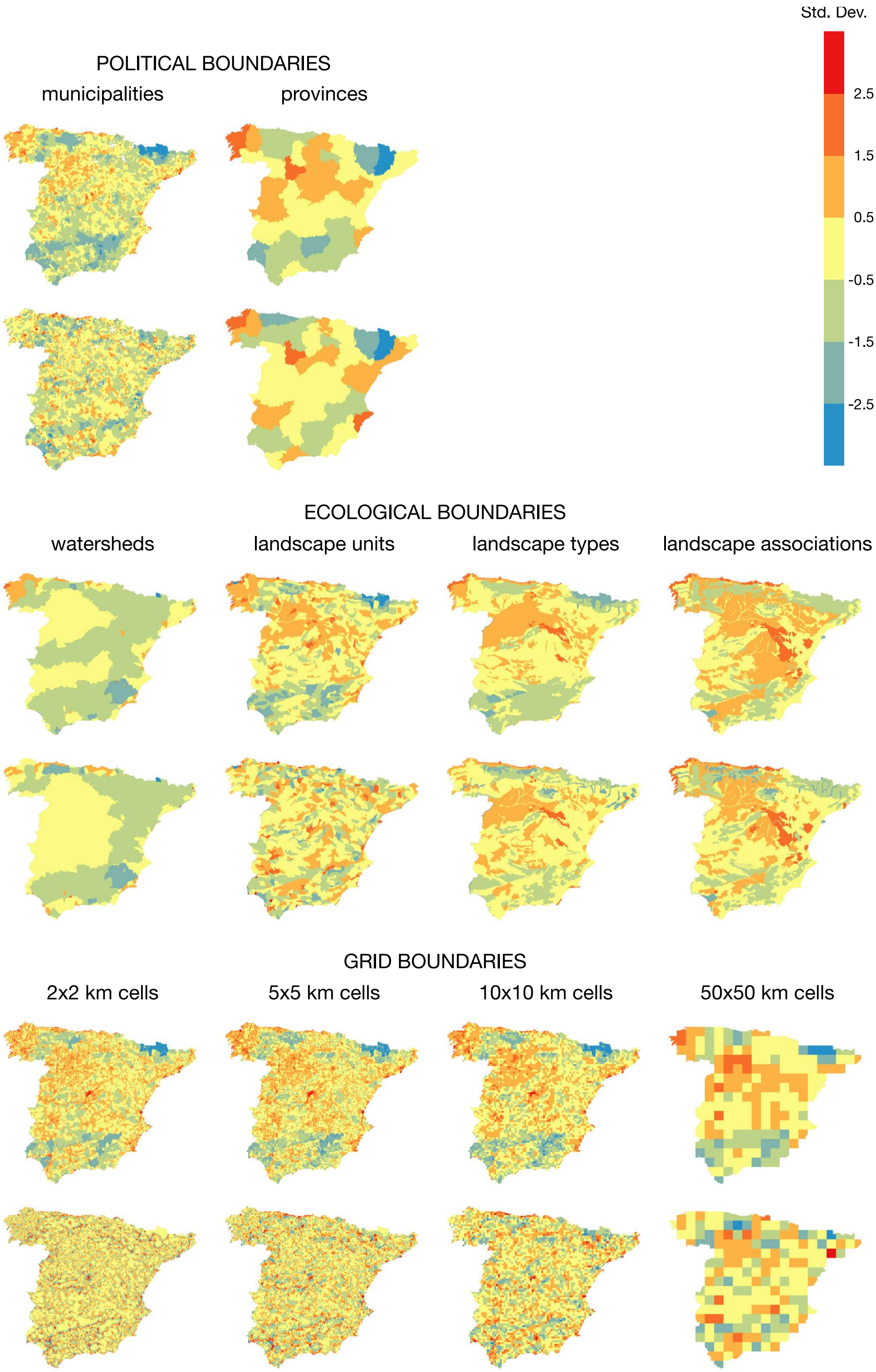


Figure S9. Mapped global (up) and local (down) residuals from DIS_2-models.

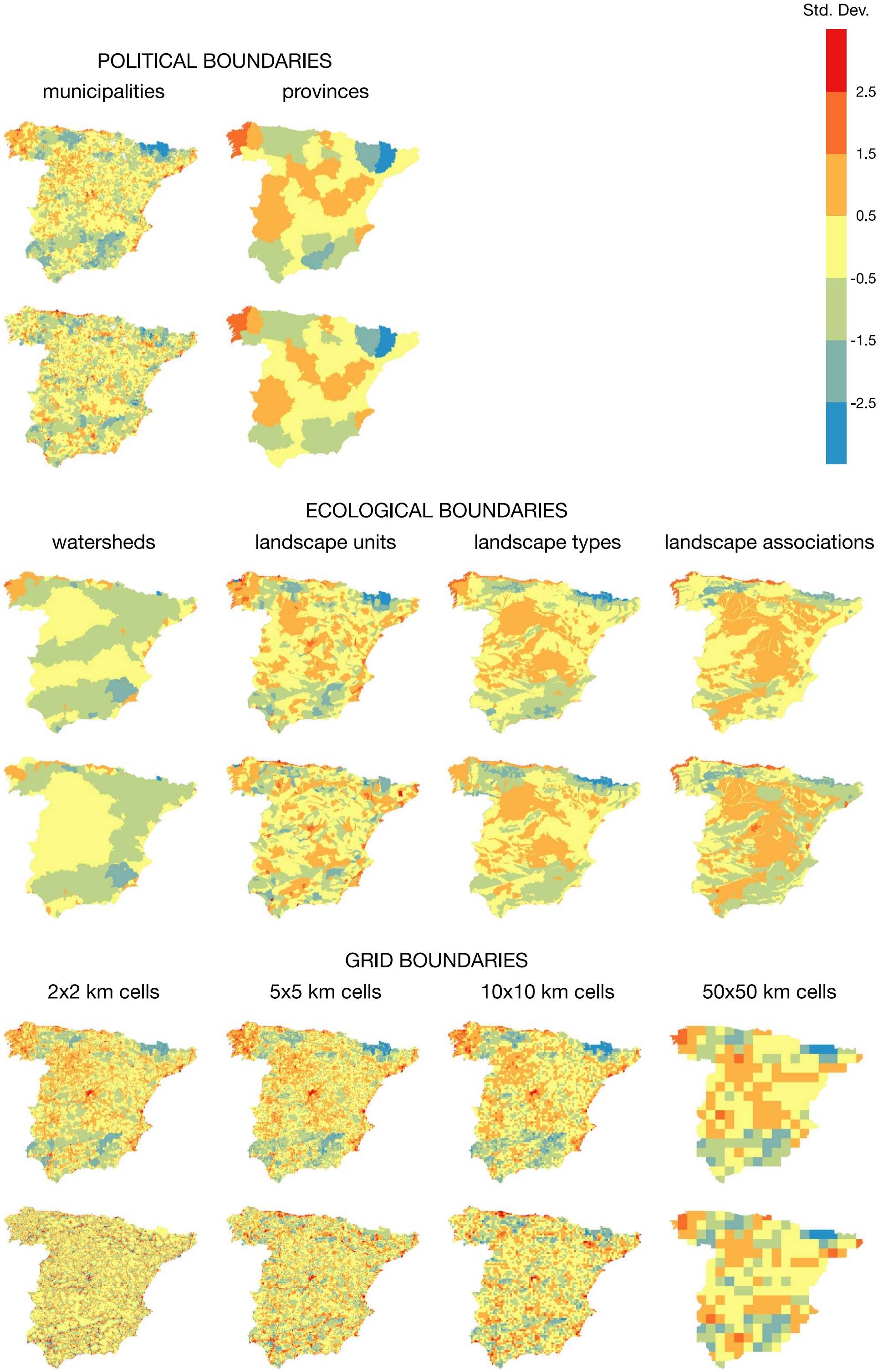


Figure S10. Mapped global (up) and local (down) residuals from DIS_5-models.

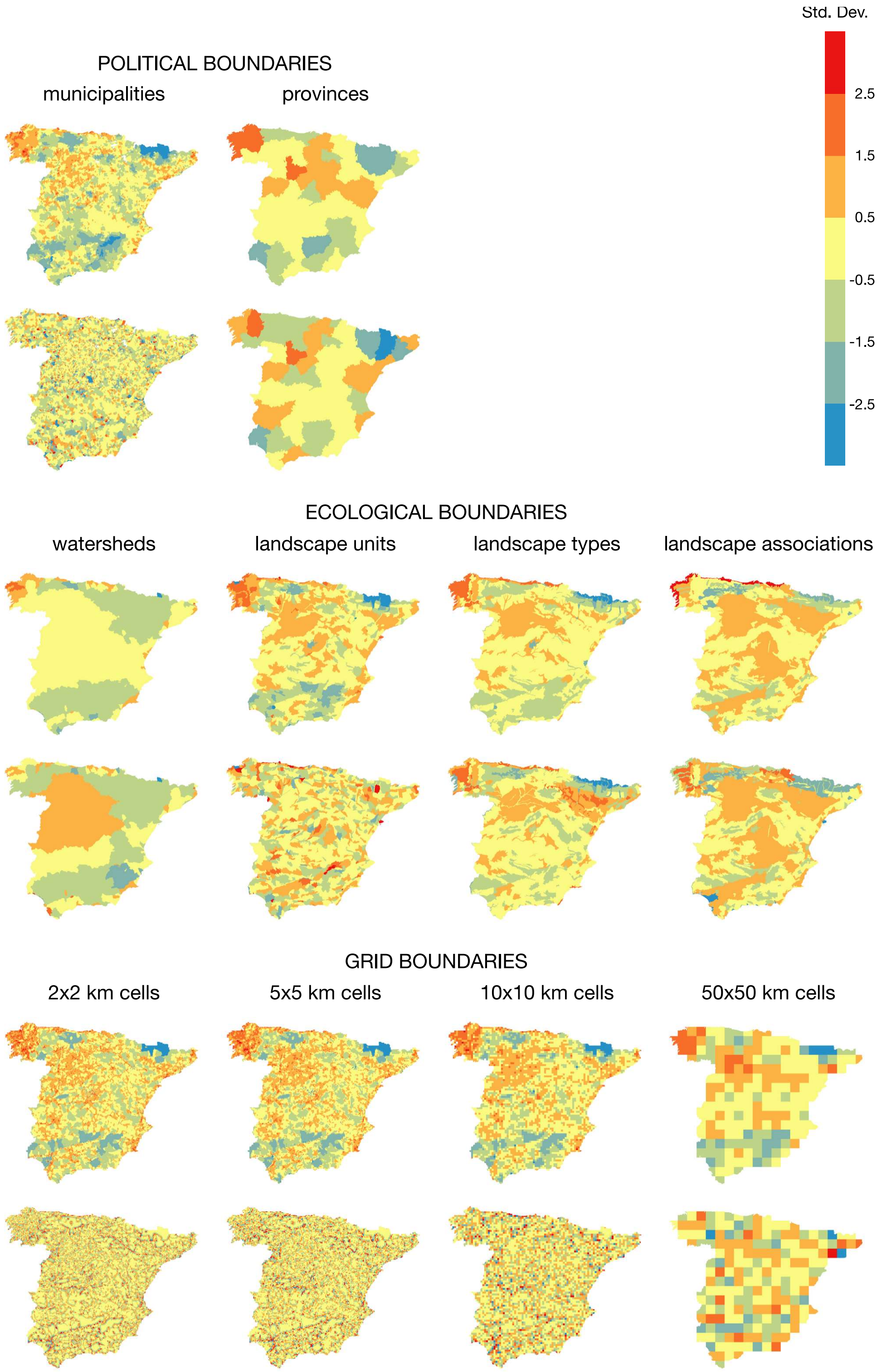


Figure S11. Mapped global (up) and local (down) residuals from UP_2-models.

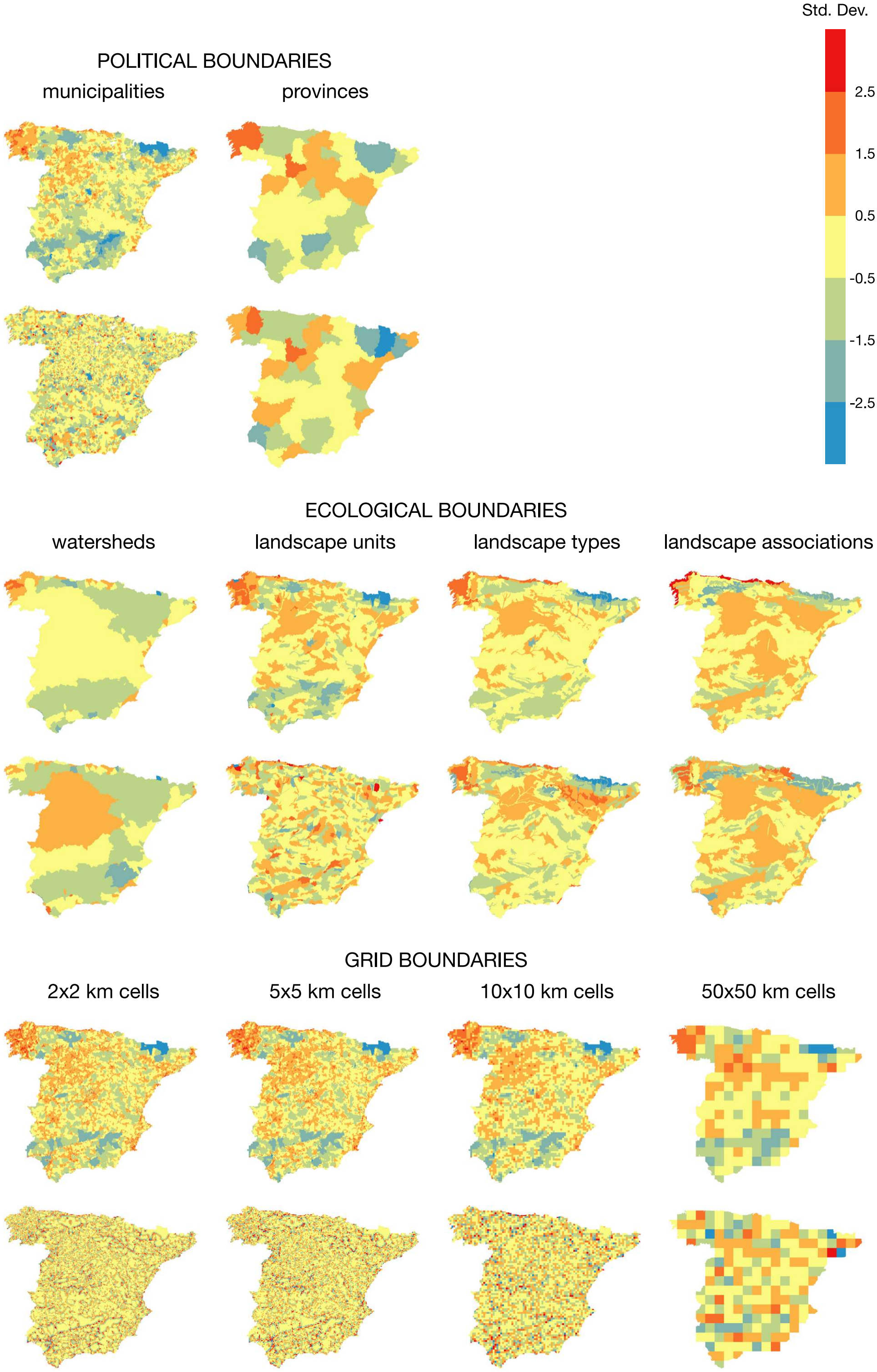
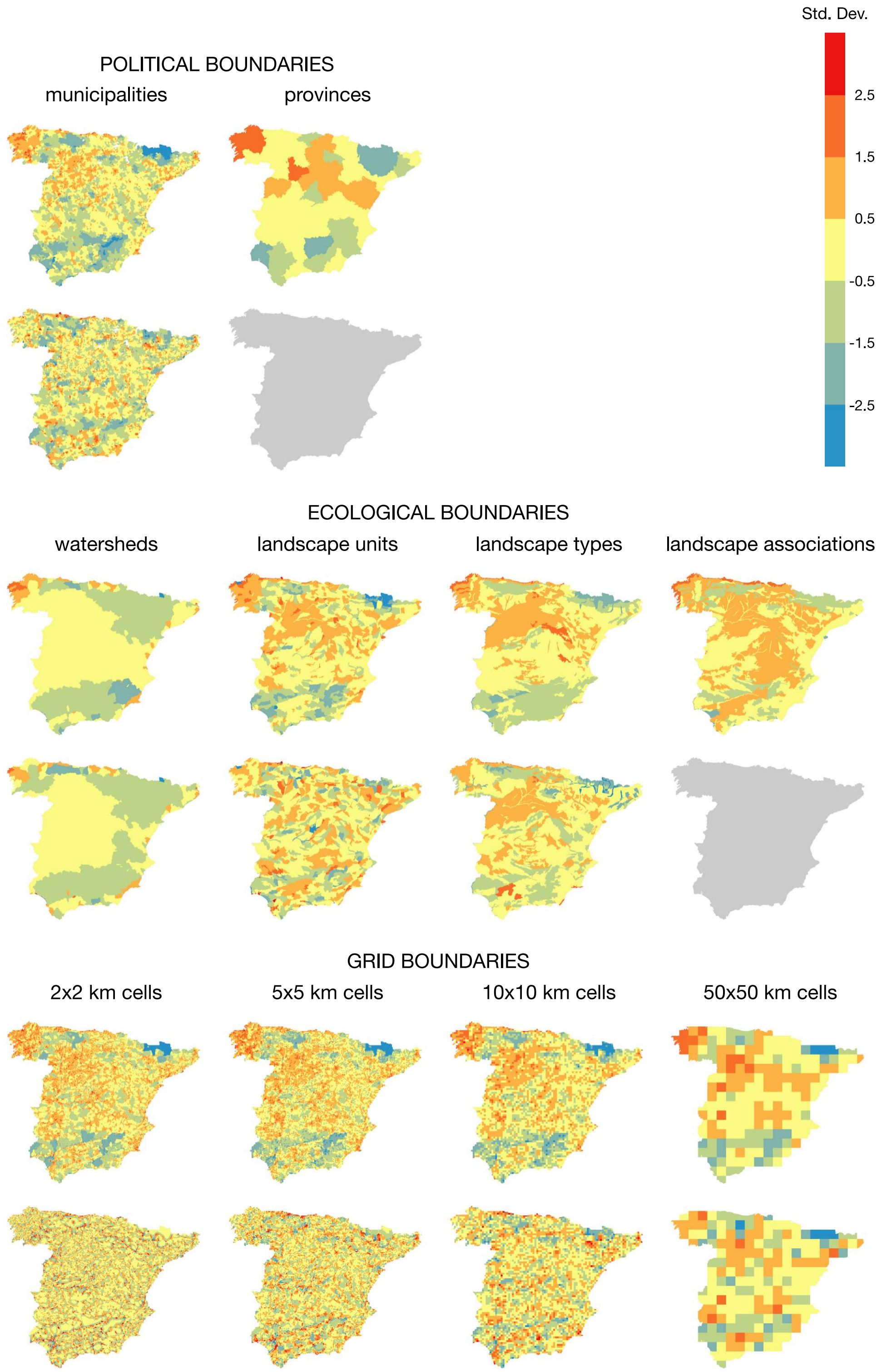
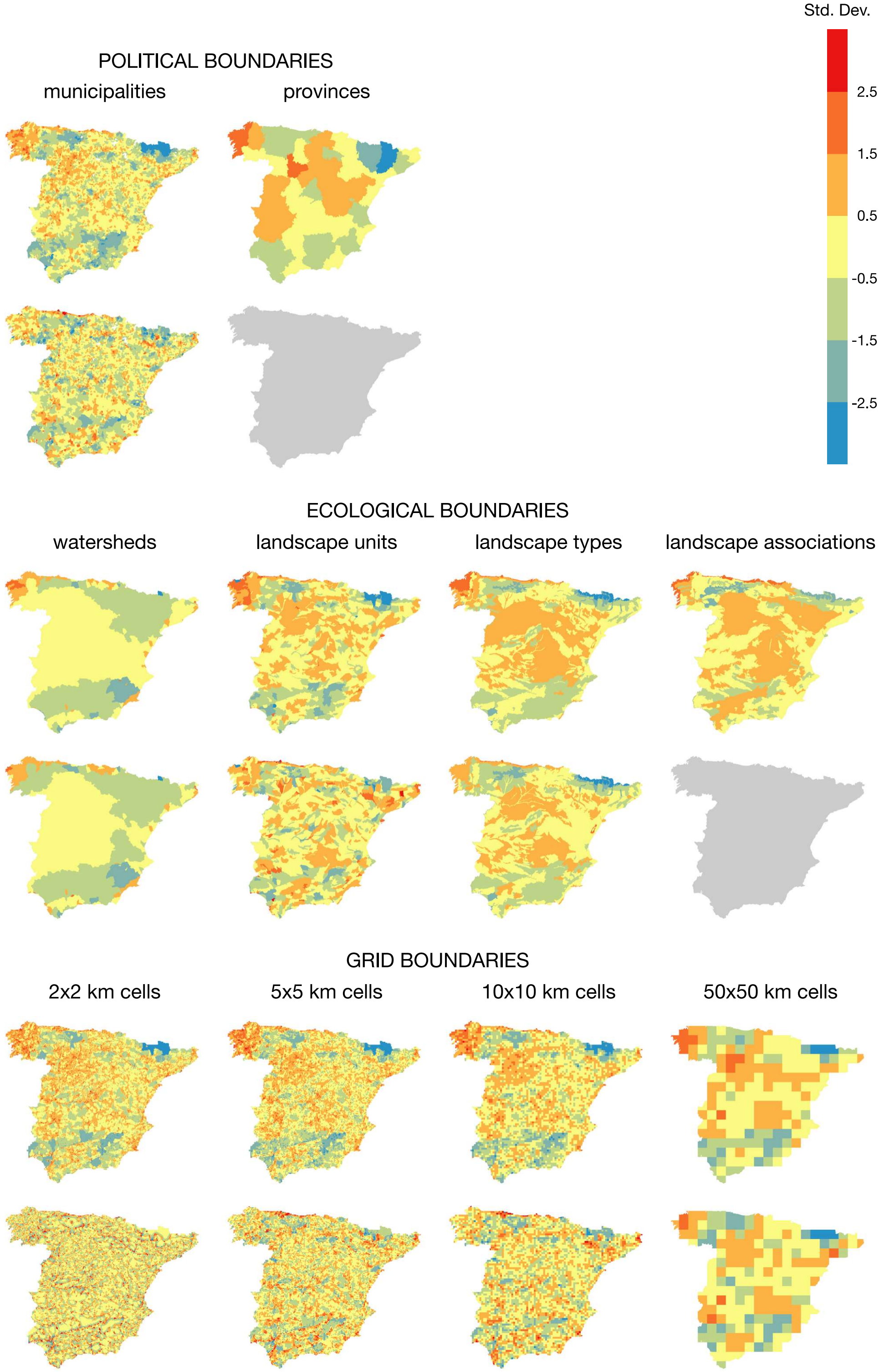


Figure S12. Mapped global (up) and local (down) residuals from UP_5-models.



igure S13. Mapped global (up) and local (down) residuals from multivariate models with *PUA* and *DIS*



igure S14. Mapped global (up) and local (down) residuals from multivariate models with *PUA* and *DIS*

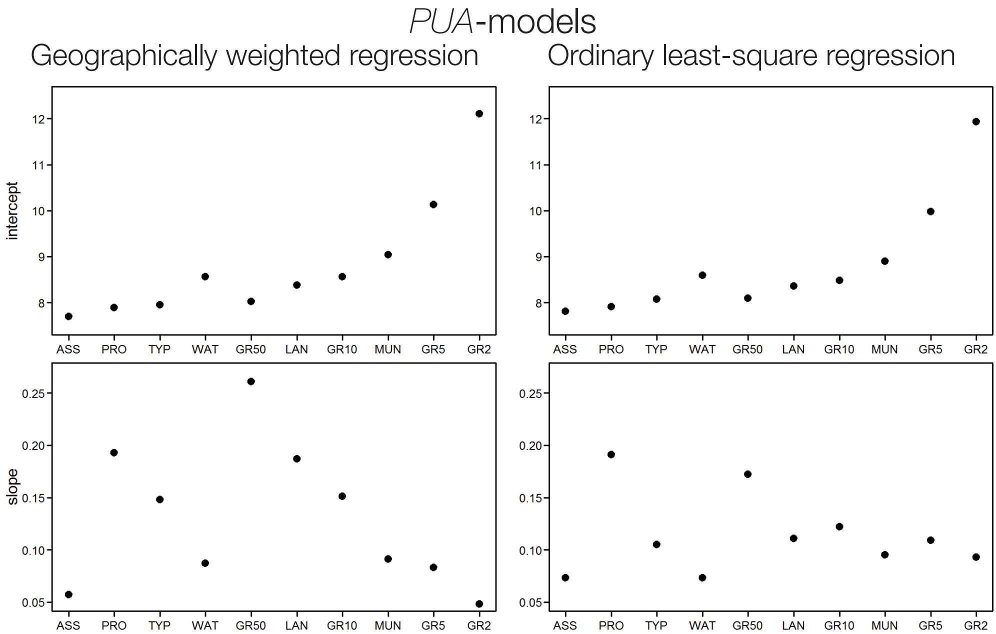


Figure S15. Representation of the coefficients estimated in the models performed with PUA (proportion of urban area) for each reporting unit (x-axis). Reporting units are ordered from left to right by decreasing size of the spatial extent (ASS=Landscape associations, PRO=Provinces, TYP=Landscape types, WAT=Watersheds, GR50=Grid units of 50x50km, LAN=Landscape units, GR10=Grid units of 10x10km, MUN=Municipalities, GR5=Grid units of 5x5 km, GR2=Grid units of 2x2 km). The units of the intercept are ln(effective mesh size per 1000 km^2 * 1000km^2 + 1).

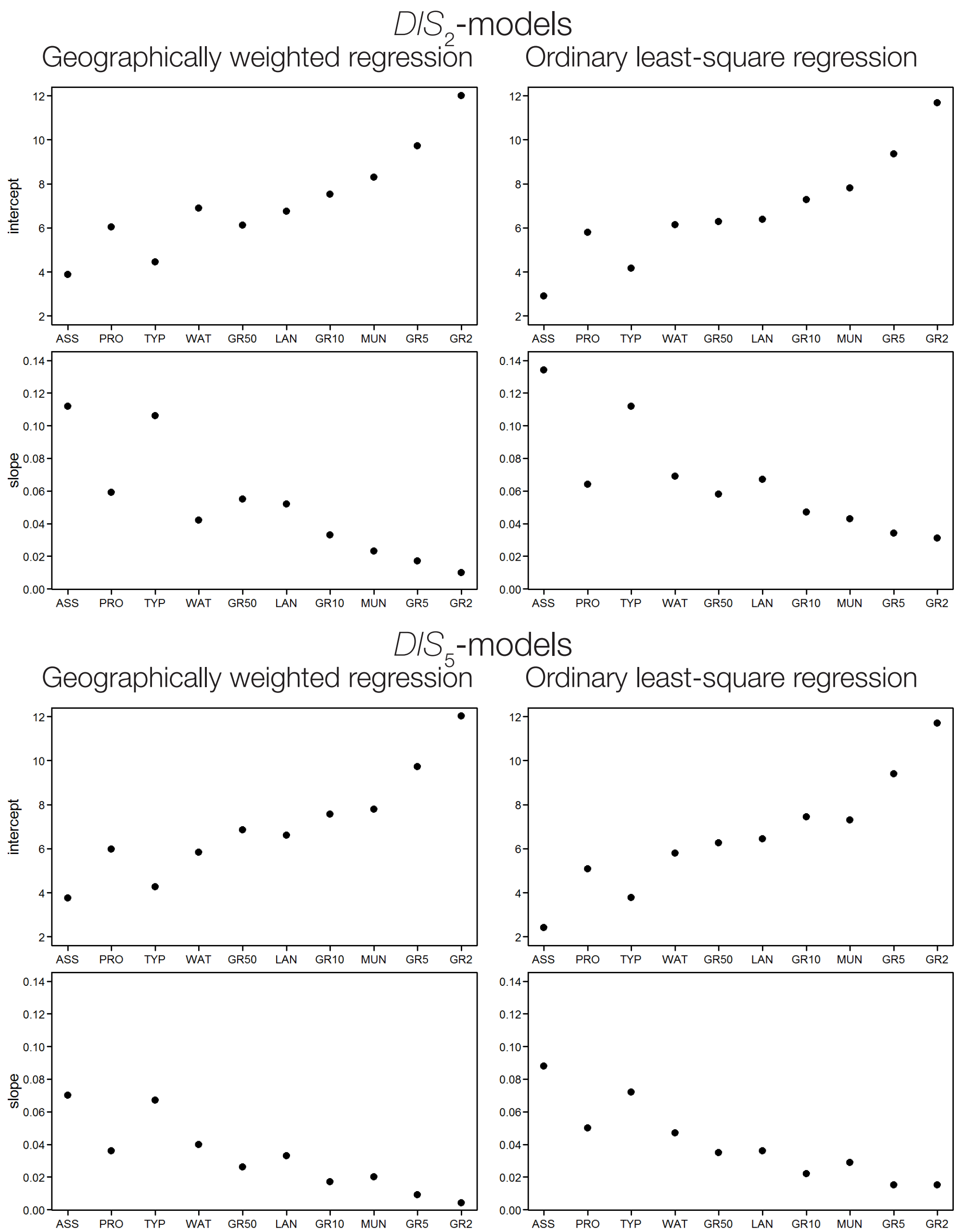


Figure S16. Representation of the coefficients estimated in the models performed with DIS_2 (degree of urban dispersion at horizon of perception = 2km) and DIS_5 (degree of urban dispersion at horizon of perception = 5km) for each reporting unit (x-axis). Reporting units are ordered from left to right by decreasing size of the spatial extent (ASS=Landscape associations, PRO=Provinces, TYP=Landscape types, WAT=Watersheds, GR50=Grid units of 50x50km, LAN=Landscape units, GR10=Grid units of 10x10km, MUN=Municipalities, GR5=Grid units of 5x5 km, GR2=Grid units of 2x2 km). The units of the intercept are ln(effective mesh size per 1000 km^2 * 1000km^2 + 1), and the units of the slope are m^2/UPU.

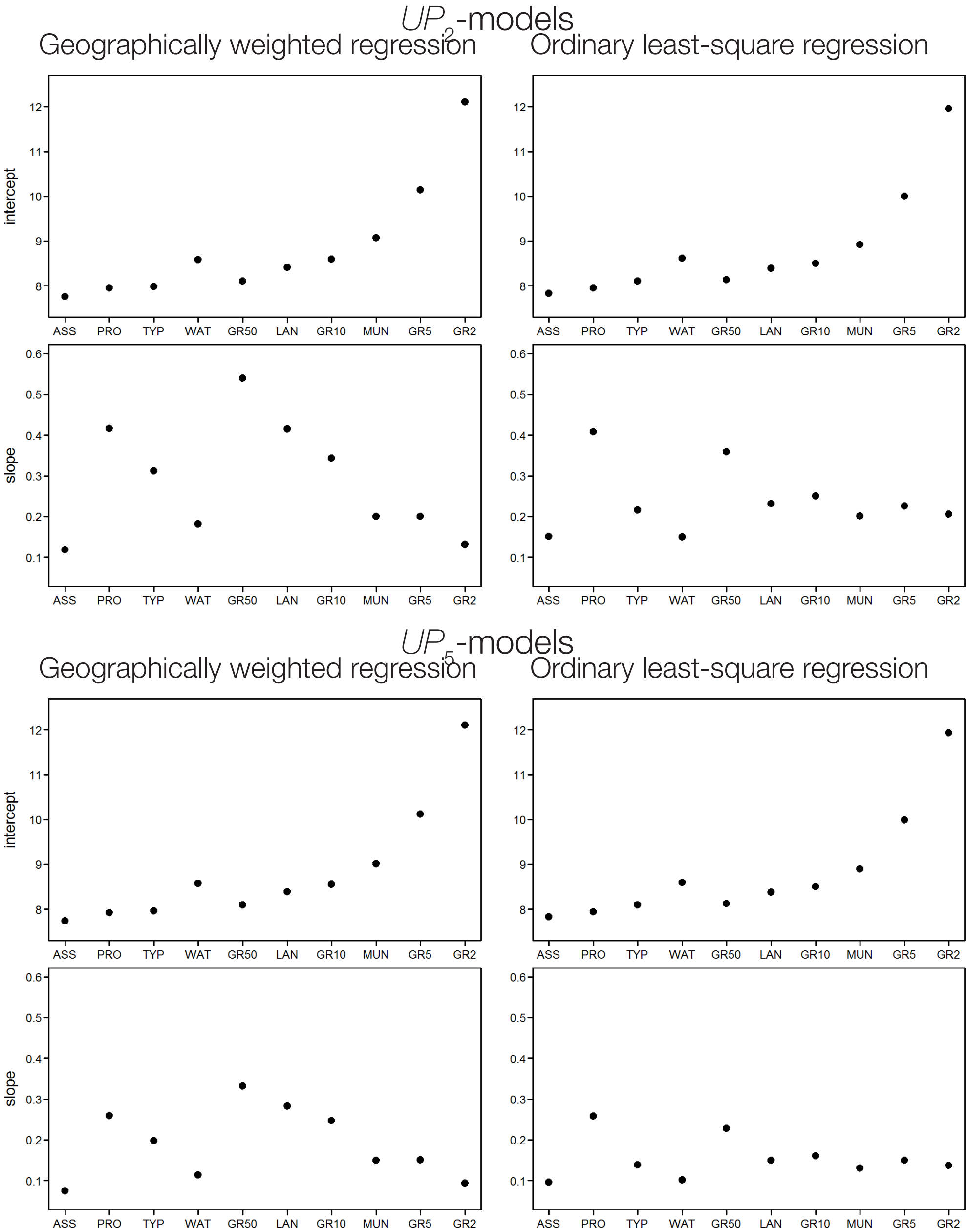


Figure S17. Representation of the coefficients estimated in the models performed with UP_2 (degree of urban permeation at horizon of perception = 2km) and UP_5 (degree of urban permeation at horizon of perception = 5km) for each reporting unit (x-axis). Reporting units are ordered from left to right by decreasing size of the spatial extent (ASS=Landscape associations, PRO=Provinces, TYP=Landscape types, WAT=Watersheds, GR50=Grid units of 50x50km, LAN=Landscape units, GR10=Grid units of 10x10km, MUN=Municipalities, GR5=Grid units of 5x5 km, GR2=Grid units of 2x2 km). The units of the intercept are ln(effective mesh size per 1000 km^2 * 1000km^2 + 1), and the units of the slope are km^2/UPU.

Chapter

Capítulo

IV

Retrasos en respuesta de las aves de medios agrícolas a los cambios en el paisaje y el clima

Resumen

Las especies que viven en zonas agrícolas han sufrido una fuerte regresión durante las últimas décadas. Normalmente se considera que la intensificación agrícola es el principal responsable de estas tendencias. Por otra parte, la dispersión urbanística, la fragmentación del hábitat y el cambio climático también son habitualmente señaladas como causas del declive de la biodiversidad a escala global. Todos estos factores pueden causar, juntos o por separado, una pérdida inmediata de especies pero también extinciones retrasadas en el tiempo. La península ibérica es una de las pocas zonas que aún conserva áreas con baja intensificación agraria y buenas poblaciones de aves amenazadas propias de sistemas agrícolas. Los objetivos de este estudio son 1) testar la existencia de retrasos en la respuesta de las aves, en relación a los cambios recientes en la estructura del paisaje y en el clima, y 2) determinar la influencia relativa de la intensificación agrícola, la dispersión urbanística, la fragmentación del paisaje y del clima en la riqueza de especies y en la amplitud de hábitat de las comunidades de aves de zonas agrícolas. Se seleccionaron un total de cuarenta paisajes de 10 x 10 km considerando todas las combinaciones posibles de valores altos y bajos de los tres predictores de paisaje (intensificación agrícola, fragmentación del paisaje y dispersión urbanística) en España. En cada uno de los paisajes, se determinó la riqueza de especies usando datos del Atlas de Aves Reproductoras y se cuantificaron los parámetros de estructura del paisaje a partir de ortofotos tomadas entre 1956 y 2001. Encontramos evidencias sólidas de retrasos en la repuesta de la comunidad de aves, siendo la riqueza actual de especies mejor explicada por valores pasados de los predictores de paisaje y clima. No está tan claro el retraso en el nivel de amplitud de hábitat de la comunidad de aves. La riqueza actual de especies está afectada negativamente por el grado de dispersión urbanística y la temperatura media de hace entre veinte y cincuenta años. La intensificación agrícola, que comenzó hace cincuenta años y ha continuado hasta hasta el presente, contribuye ligeramente a aumentar la riqueza de especies, pero fundamentalmente ha determinado una disminución en la amplitud de hábitat promedio de la comunidad de aves, i.e. un aumento relativo de las especies más adaptadas al cultivo cerealístico en el presente. La

fragmentación del hábitat entre 1980 y el presente contribuye a aumentar la proporción de especies generalistas, compensando en parte la disminución relativa de esas especies causada por la intensificación agrícola. En general, nuestros resultados sugieren que las decisiones en conservación basadas en el análisis de cómo responden las especies a valores actuales de paisaje y clima son probablemente insuficientes para prevenir la pérdida de especies en el futuro.

Torres, A., Jaeger, J.A.G., Carrascal, L.M, Alonso, J.C. Time-lags in farmland bird responses to landscape and climate changes. In preparation.

Time-lags in farmland bird responses to landscape and climate changes

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Abstract

Species living in farmland have suffered severe declines during the last decades. Agricultural intensification is usually considered the main driver behind these trends. Also, urban sprawl, landscape fragmentation, and climate change are commonly highlighted as additional causes of global biodiversity declines. All of them, together or separately, can cause the immediate loss of species but also time-delayed extinctions. The Iberian Peninsula is one of the few areas that still preserves areas with low-intensity farming and good populations of many threatened farmland birds. The objectives of this study were 1) to test for the existence of time-lags in the response of birds, which could be related to present or past changes in landscape structure and climate, and 2) to determine the relative importance of agricultural intensification, urban sprawl, landscape fragmentation, and climate on the richness and habitat breadth of the bird communities of agricultural landscapes. A total of forty 10 x 10 km plots accounting for all possible combinations of values of the three main predictors (agricultural intensification, landscape fragmentation, and urban sprawl) were selected in Spain. At each of these 40 plots we determined bird species richness using data from the Breeding Bird Atlas, and landscape structure parameters from digital orthoimages taken between 1956 and 2001. We found strong evidence for time-lag responses in the farmland bird community, with present-day species richness being better explained by past values of landscape and climate predictors. A time-lag in the functional response of the bird community was less clear. Present-day species richness was negatively affected by the degree of urban sprawl and the mean temperature twenty-fifty years ago. The agricultural intensification starting fifty years

ago and continuing up to present also slightly contributed to increase current species richness, but mostly determined a decrease in the mean habitat breadth of the bird community, i.e. a relative increase of those species most adapted to cereal farmland at present time. Landscape fragmentation occurring between 1980 and present time contributed to increase the proportion of generalist species, compensating in part for the relative decrease in these species caused by intensive farming. Overall, our results suggest that conservation decisions based on the analysis of how species respond to present-day landscapes are likely insufficient to prevent species losses in the future.

KEYWORDS Agricultural intensification, birds, climate change, extinction debt, landscape change, fragmentation, species richness, urban sprawl.

Introduction

As a result of an age-old co-evolution between farmland and natural habitats in the Mediterranean basin, agricultural landscapes of this region harbor an extraordinary biodiversity (Ruiz 1990; Tucker et al. 1994; Farina 1997). However, farmland is today the ecosystem with the highest proportion of bird species with unfavorable status, since many of them have recently suffered severe declines. The loss of bird diversity has been quantified at more than 300 million breeding species over the last three decades (EBCC 2009).

Agricultural intensification has been identified as the main cause contributing to the decline or extinction of many European farmland bird populations (Donald et al. 2001; Benton et al. 2003). A traditional management of agricultural landscapes persisted well into the second half of the 20th century (Santos & Suárez 2005). Since the 60's, these landscapes were substantially modified by agricultural intensification (Suárez 2004). This process mostly conducted towards a simplification of the landscape structures and an increased use of fertilizers and pesticides, which lead to a reduction in the availability of resources for wildlife (Benton et al. 2003; Ewald et al. 2015).

During the same period, other important processes have susbtantially modified Mediterranean farmland. One of them is urban expansion, which has affected the Mediterranean basin more than any other biodiversity hotspot in the world (Seto et al. 2012). The dissemination of built-up areas (urban sprawl) is becoming increasingly common and not only restricted to metropolitan areas (Brown et al. 2005; EEA 2006). The Mediterranean region also has an ancient and widespread road-network that affects both, protected areas and threatened species (Ferreras et al. 1992; Gomes et al. 2009; D'Amico et al. 2015). There is growing evidence that roads and settlements reduce wildlife populations by (i) increasing mortality, (ii) decreasing the extent and quality of appropriate habitat, and (iii) fragmenting populations into smaller sub-populations, which are easily vulnerable to local extinction events (Fahrig & Rytwinski 2009). However, very little is known about the relative contribution of these drivers of landscape change to the decline of biodiversity in agricultural areas. Compared to other habitats, farmland has been identified as the most exposed to transport infrastructure and built-up areas in Spain (Torres et al. subm. Chapter 2), and a growing number of studies are evidencing the deleterious effects of these structures on farmland birds (e.g., Torres et al. 2011).

A second process that has strongly influenced species distributions and population trends is climate change (Thomas & Lennon 1999; Parmesan & Yohe 2003; Brommer 2004). Global temperatures have increased by 0.7 ºC since the beginning of the 20th century (IPCC 2007). This global warming is driving many species out of their thermal equilibria and changing their abundances, distribution and phenology (Lenoir & Svenning 2013; Pavón-Jordán et al. 2015). Therefore, the temperature increase due to climate change should be taken into account when examining the effect of land-use intensification on bird communities.

Community responses to landscape changes have to be understood in two dimensions, temporal and structural. On the temporal dimension, species do not necessarily go extinct immediately when either their habitat shrinks, the climate changes beyond their tolerance limit, or an invasive species spreads, but might do so with a significant delay (Tilman et al. 1994; Kuussaari et al. 2009; Dullinger et al. 2013). Such time-lags between disturbance pressure, population decline and, finally, extinction create a transient disequilibrium between environmental conditions and a species' range size. The number of species that face extinction as a function of past and present pressures has been called the 'extinction debt' (Tilman et al. 1994). Based on the conceptual model of extinction debt (Kuussaari et al. 2009), and using species richness as the first main response variable of the bird community, we predicted that goodness of fit of the models performed to explain species richness should rank higher with predictor variables at different time periods depending on the degree of time-lag in the response of the species (Fig. 1). After a landscape or environmental perturbation, reaching a new equilibrium may take

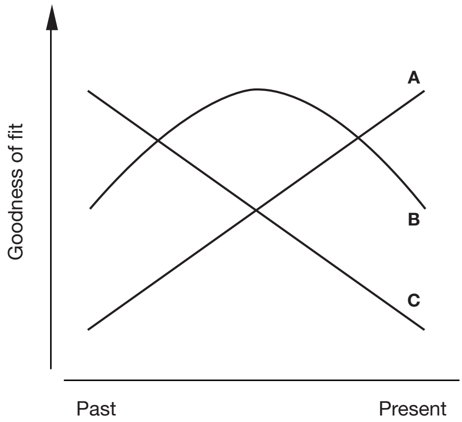

Figure 1. Goodness of fit of the models performed with current species richness (or other biological response) and predictor variables measured at three time points would rank lower or higher depending on the degree of time-lag in the response of the species. Trend A corresponds to a species (or species assemblage) with fast or immediate response, whereas trend B corresponds to a species with a moderate time-lag in its response, and trend C correspond to a species with a long time-lag in its response.

a short time, e.g. when the perturbation causes the immediate extinction of the species, or a long time if the species has a time-lagged response. When modeling the abundance of species with fast or immediate response, predictor variables describing current environmental conditions should rank higher than those describing past conditions (Fig. 1A). In contrast, in the case of species with a time-lagged response, models performed with predictor variables describing past environmental conditions would explain the current species' abundance better than models using predictors for the present conditions, which suggests a possible extinction debt (Fig. 1B, for species with a moderate time-lag in their response, Fig. 1C for species with the highest time-lag).

As for the structural dimension, a major response of a community to landscape disturbances is a biotic homogenization, i.e. a decrease in the functional diversity among species that constitute the community (Olden & Rooney 2006; Devictor et al. 2008a). Ecological processes leading to homogenization need not necessarily include either species invasion or extinction (Olden & Poff 2003). Such processes rather promote the dominance of some, usually widespread and easily adaptable, species and the decrease or extinction of others, mostly rare and specialist species. Simplified landscapes created by intensive land-use can be particularly detrimental to habitat specialists (Ekroos et al. 2010). Yet, driving forces of functional homogenization in bird communities as a result of multiple changes have barely been investigated at large scales (Devictor et al. 2008a).

Our objectives in this study were twofold. First, we tested our predictions of the variations in the goodness of fit across time in relation to changes in landscape and climate, using species richness and the habitat breadth of the bird community as response variables. Second, we estimated the relative importance of different drivers of environmental change – namely, agricultural intensification, urban sprawl, landscape fragmentation, and climate change – in determining the current structure of farmland bird communities in the Iberian Peninsula. The relative importance of these factors in causing bird declines in agricultural landscapes is unknown. However, in order to reverse these negative trends it is crucial to identify the specific driving forces behind them. This will lead to better understanding how fundamental changes in the structure of bird communities occur, and thus help defining more effective conservation strategies for farmland biodiversity.

These objectives concern processes which (i) operate at regional and even macroecological scales, and (ii) might be interacting to generate spatial patterns. Successfully meeting these objectives thus requires an experimental design at a large scale, an always difficult and often even impossible task (Blackburn & Gaston 2003). Here, we used a landscape-scale experiment (*sensu* Brennan et al. 2002) to test our predictions of the responses of the farmland bird community in the Spanish sector of the Iberian Peninsula. Dry cereal farmland constitutes a stronghold for a large proportion of farmland and steppe birds (Santos & Suárez 2005). Overall, Spanish rural land use is characterized by extremes – large areas of land are under very low-intensive farming, while many other areas are subjected to intensive agriculture (Santos & Suárez 2005; Beaufoy et al. 2012). In addition, 50% of the land in Spain lies within 869 m of a transport infrastructure and 1.6 km of a built-up area (Torres et al. subm. Chapter 2). Indeed, Spain is the European country with the longest motorway network and no other EU country has experienced such rapid expansion of this infrastructure in the last decades (Holl 2011). Thus, Iberian dry open farmland is a suitable system for studying the effects of different drivers of environmental change on the bird community.

Methods

Landscape experimental design

We used a quasi-experimental approach to sampling landscapes. Landscapes are not manipulated but are chosen using strict, non-random selection criteria to ensure a wide range of values of the landscape predictor variables and to avoid correlations among them, thus increasing the power of statistical inferences (Brennan et al. 2002). There are many different farming contexts worldwide. We mainly focus on the flat, open landscapes created by the extensive cultivation of cereals on a rotational basis, which constitutes the most common farming landscape in Spain.

The candidate landscapes corresponded to the breeding bird atlas 10 x 10 km UTM cells. Cartographic distortions or boundaries caused some squares to be somewhat less than 100 km^2. We considered cells (i) larger than 80 km2, (ii) selected among a subsample of bird distribution cells of high reliability according to (Carrascal & Palomino 2012), (iii) mostly distributed in the main Mediterranean bioclimatic stages of the peninsula: Supramediterranean, Mesomediterranean and Thermomediterranean bioclimatic domains (Rivas-Martínez 1981), (iv) whose mean height were above 10 m and below 1,200 m (obtained from a 25 x 25 m DEM), (v) whose mean slope below 15% (obtained from a 25 x 25 m DEM), and (vi) for which the area of arable fields was higher than 25% based on SIOSE project (Spanish Land Cover and Use Information System, 2005; 1:25,000 scale; National Geographic Institute of Spain 2005).

For the resulting landscapes, we quantified agricultural intensification (as the mean *area-to-perimeter ratio*; see detailed information of the indicators used below) from SIGPAC (a GIS facility for Common Agricultural Policy information sponsored by the Spanish Ministry of Agriculture), and obtained estimates of landscape fragmentation and urban sprawl indicators from Torres et al. (subm. Chapter 3). We classified every landscape according to their values for each indicator. For example, landscapes with values of agricultural intensification in the lower third of the frequency distribution were considered to have a low level of intensification, whereas landscapes with values in the upper third were considered to have a high level of intensification. Then, we used a randomized stratified sampling design to select landscapes representing all possible combinations of low and high levels of each landscape variable to avoid correlation among variables (Fig. 2). We considered between 3 and 7 replicates of each of eight combinations of two intensity levels of the three drivers of landscape change. The effect of spatial

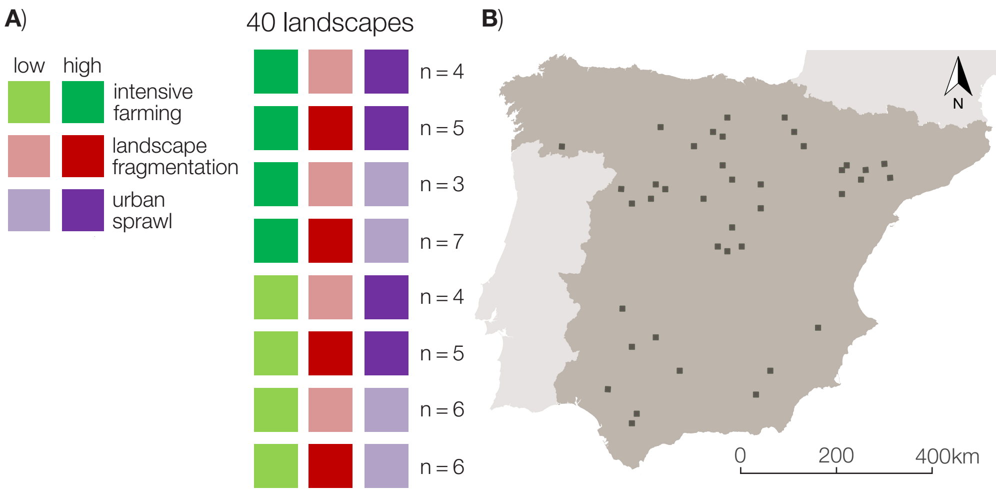

Figure 2. (A) Illustration of the possible combinations of low and high levels of each of the three landscape predictor variables considered, and sample sizes of the eight resulting types of landscapes. (B) Location of these 40 landscapes (black dots), represented by 10 x 10 km plots selected for analysis in Spain.

autocorrelation was reduced by selecting landscapes of the same treatment separated from each other by at least 20 km.

Landscape dynamics

In each landscape, we quantified agricultural intensification, urban sprawl, and landscape fragmentation for 1956, 1980, and 2001. The first time point (1956) corresponds to a situation before any drastic transformation of the traditional farming systems in Spain has happened and thus represents the original situation. Though we had values of agricultural intensification, sprawl, and fragmentation from the previous landscape sampling, the same sources were not available for the past. To be able to draw solid comparisons of the values of these drivers throughout time, we quantified indicators for each time point following the same procedure. To quantify predictor variables we used digital orthoimages of 1956, 1980, and the time of the Breeding Bird Atlas surveys (1998-2001), or at the nearest time possible to each of these three years. Most of the digital orthoimages used were compiled, treated, and put available via web map services (WMS) by regional agencies of geospatial information (Table S1). For those areas where digital orthoimages were not available, we obtained the digital aerial photographs from the National Geographic Institute of Spain and processed them in ArcGIS (ESRI).

Resolution of the digital orthoimages ranged between 1 and 0.25 m, and the scale between 1:5,000 and 1:10,000.

Predictor variables

We quantified one climatic and four landscape metrics by means of well-known indicators.

Agricultural intensification

Agricultural intensification has many components, such as loss of landscape elements, enlarged farm and field sizes and increased inputs of fertilizers and pesticides. We used field size as a proxy for agricultural intensification. Field size is the area of an individual plot of cultivated land. Plots of cultivated land are demarcated by transitions to other landscape elements or to adjacent plots of cultivated land. This measure highly differs between low-intensity and high-intensity agriculture (Karp et al. 2012). Increases in field sizes are often coupled with decreasing densities of small biotopes, field divides and density of hedgerows (Levin 2006). In contrast, changes with decreasing field sizes are coupled with increasing densities of field divides and small biotopes. Moreover, there is a positive relationship between field size and farm size (Levin 2006), and between farm size and income (Berry 1972), and it has been suggested as a valid surrogate for mechanization and labour intensity (Kuemmerle et al. 2013). Instead of the direct field size, we calculated the *area-to-perimeter ratio* (*AP*) because it captures the mean size and shape of the fields holding constant the total number of fields. Increases in the mean *AP* reflect increasing intensification, while decreases reflect either increasing complexity of field shapes or the enlargement of the fields. To quantify mean *AP* in each landscape, we digitized all fields in 5 non-overlapping plots of 1 x 1 km randomly distributed in the landscapes, but similar throughout time. Every field contained or intersected in the plot was digitized in its total extent. When any of the plots did not fall in an agricultural area a new random plot was selected.

Urban sprawl

We considered urban sprawl along a continuous gradient rather than distinguishing only urban or rural sprawl from non-sprawl. Only those traffic areas that are located within the settlements were included. We quantified urban sprawl with the *degree of urban dispersion* (*DIS*), since it is the metric that better capture the spatial arrangement of built-up area (Jaeger et al. 2010a). Thus, urban sprawl increases with higher dispersion of built-up area (Jaeger et al. 2010b). *DIS* is based on the distances between any two points within the built-up areas in the landscape (for all possible pairs of points within and between built-up patches). The maximum distance up to which point-to-point distances are measured is the *horizon of perception* (*HP*) (Jaeger et al. 2010a). We used an *HP* of 2 km and applied the cross-boundary connections procedure (Moser et al. 2007), where the settlement pattern outside the reporting unit but within the *HP* also influences the values of the metrics. Thus, we digitized built-up areas over the orthoimages, irrespective of their use, with a minimum mapping unit of 15 x 15 m, for each landscape and a buffer of 2 km. *DIS* is weighted with an effort function so that the farther apart the two points from each other, the higher their contribution to *DIS*, and the higher the effort required to connect them (Jaeger et al. 2010a). This is expressed in urban permeation units (UPU) per m^2 of urban area. The minimum possible value of *DIS* (0 UPU/m^2) is found when there is no built-up area in the reporting unit. The maximum values of *DIS* are reached when each built-up patch is located away (evenly dispersed) from all other built-up patches (according to the scale of analysis of sprawl). When new buildings are added within the existing built-up areas (densification), the values of *DIS* do not change.

Landscape fragmentation

Over the digitized map of built-up areas we also digitized paved roads and railways to delineate a map of fragmenting features. Given that orthoimages for 1956 and 1980 are non-color, it was sometimes difficult to differentiate between paved and unpaved roads. Thus, for these time points we compared the orthoimages with the road maps for 1960 and 1980 at 1:800,000 scale (Spanish Ministry of Development).

We applied the *effective mesh size metric* (m_{eff}) (Jaeger 2000) to quantify landscape fragmentation, following the cross-boundary-connections procedure in which reporting unit boundaries do not fragment the landscape (Moser et al. 2007). We considered another cell around the core cell (i.e., the 8 neighbor cells) for the digitization of transport infrastructure. This metric is based on the probability that any two points chosen randomly in an area are connected and are not separated by any barriers. This leads to the formula:

$$m_{\text{eff}}^{\text{CBC}}(\text{unit } j) = \frac{1}{A_{tj}} \sum_{i=1}^{n} A_{ij} \cdot A_{ij}^{\text{cmpl}},$$

where n is the number of remaining patches i (not urban), A_{tj} is the total area of reporting unit j, A_{ij} is the area of patch i inside of reporting unit j and A_{ij}^{cmpl} is the complete area of patch i including the area outside the boundaries of reporting unit j. The smaller the m_{eff}, the more fragmented the landscape. The largest possible value of m_{eff} is the size of the region studied when the landscape is unfragmented (in our case 900 km^2). The smallest value of 0 km^2 indicates complete fragmentation, i.e., no suitable area left. However, the m_{eff} measure reacts more slowly to increasing fragmentation as it approaches 0 km^2. To avoid this effect, we also calculated the *effective mesh density* $s_{eff} = 1/m_{eff}$, which is more suitable for detecting and comparing slopes in graphs (Jaeger 2000, 2002; Jaeger et al. 2007). The value of s_{eff} was expressed as the effective number of meshes per 100 km^2. The higher number of meshes, the more fragmented the landscape.

Percentage of croplands

Landscape may differ considerably in terms of the amount of arable land throughout landscapes and time, since some fields might become abandoned or instead semi-natural areas become cultivated. Thus, to control the effects of this heterogeneity source we incorporated the *percentage of croplands* in the landscape as a control variable. Changes in this variable were quantified through two land-cover maps roughly matching the time periods studied: (1) the forest map of Spain developed by Ceballos and based on the aerial photograph of 1956 (1966; 1:400,000), and (2) the "Mapa de cultivos y aprovechamientos" (MCA; Spanish Ministry of Agriculture; 1:50,000) for 1980 and 2000. The existing agricultural land cover classes from MCA were integrated into a single layer of croplands to allow comparisons with Ceballos' map. All landscape metrics were quantified in ArcGIS (ESRI).

Climate change

We included *mean temperature* (T) as an explanatory variable, using outputs of a readily available dynamic downscaling of the climate for the Iberian Peninsula at 5 km horizontal resolution between 1950 and 2009 (Dasari et al. 2014). We used 5-year air temperature averages to account for climate in our study considering 1955-1960, 1975-1980, and 1995-2000 intervals.

Species data

Information on current species distribution of breeding birds was provided by the Breeding Bird Atlas (Martí & Del Moral 2003), the most current and detailed source of information for breeding bird ranges in Spain. The sampling strategy consisted in extensive surveys in 10x10 km UTM cells, during spring in the period 1998-2001. The presence or absence of individual species was reported for each cell.

To calculate the habiat breadth of the bird community the densities of each species in different types of habitats are required. These were obtained from Carrascal & Palomino (2008). These densities refer to 74 habitat-regions distributed in eight bioclimatic strata in the Iberian Peninsula, and belonging to 25 main habitats. This broad array of habitats include six different agricultural landscapes (from dry extensive cereal fields, to olive groves, and complex agricultural mosaics), two types of urban environments (from dense, large, cities to less populated areas with scattered buildings), three kinds of herbaceous habitats and three types of scrublands according to position within the altitudinal gradient, freshwater marshlands, open juniper woodlands and scrublands, sclerophyllous woodlands (mainly holm oak forests and parklands), riverbank copses, three kind of pinewood forests according to elevation and two types of deciduous forests (oakwoods and beechwoods). These 25 habitat categories were reduced to 14 major habitats, which were more appropriate for the purposes of this study (Table S2). For each of these 14 habitats, the maximum density of each species was recorded considering the 74 habitat-region categories. This selection process of maximum densities avoids the consideration of zeros for characterizing the abundance in an habitat category in a region that is outside the geographical range of each species, and refers to the maximum ecological density a species may attain in an habitat category at the large-scale within continental Spain. The densities in Carrascal & Palomino (2008) account for differences in detectability among species obtained from a large scale census program using stationary point counts of a duration of 5-min. A large sample of 12,068 point counts were censused an average of 1.8 years (2004-2006) in 594 UTM 10 x 10 km cells throughout continental Spain.

Then, for each species we defined the following variables depicting their habitat preferences: maximum ecological density registered in continental Spain (in birds/km^2); average, standard deviation and coefficient of variation of the maximum densities measured in the 14 major habitat categories;

habitat breadth in the 14 habitat categories using Levin's index; and an index of habitat preferences for extensive cereal fields. The index of habitat preferences was obtained by dividing the maximum densities observed in the habitats belonging to this landscape category by the maximum ecological density registered in the whole sample of 74 habitat-regions categories in continental Spain. For those species that were missing in Carrascal & Palomino (2008) we conducted an extensive literature survey to get densities per habitat. Habitat breadth (*HB*) of species in the above mentioned 14 major habitat types was calculated following Levins (1968) index divided by the number of habitat categories:

$$HB = \frac{[(\sum pi^2) - 1]}{14},$$

Where pi is the proportion of the density for each species measured in the habitat i (dividing density in habitat i by the sum of all maximum densities recorded in the 14 habitat categories). This index ranges between 1 (evenly distributed across the 14 habitats) and 1/14 (only present in one habitat). We calculated median habitat breadth for each landscape based on the individual habitat breadth values of the species present as a community index (sensu Julliard et al. 2006).

There are many bird species that use farmlands to a variable extent. For instance, birds that feed in farmlands, nest in croplands or birds that benefit from secondary habitats (hedges, bushes, buildings, isolated trees or small wetlands). At the landscape scale (10x10 km cells) these species have a marked tendency to occur together, despite the notable difference in their local habitat selection patterns (Santos & Suárez 2005). Yet, the relative importance of the predictor variables might differ depending on the set of species considered. Thus, we differentiated three groups of birds depending on their habitat preference for extensive cereal fields (Table S3) to quantify species richness and HB: (i) species with a high preference (SPP1: $\geq$ 75%, n = 22; these are the more specialized, typical steppe birds), (ii) species with high and moderate preference (SPP1,2: $\geq$ 50%, n = 39), and (iii) species with high, moderate, and low preference (SPP1,2,3: $\geq$ 25%, n = 75). In the main text we present the results for the second group but for species with higher and lower preference for extensive cereal fields the results are also provided in the supplementary material.

Statistical analyses

Relationships between current species richness or median habitat breadth and the predictor variables for 2001, 1980, and 1956 were analyzed by means of multiple linear regression models, using the information-theoretic model comparison approach. Models for 2001 and 1956 were compared with Akaike's second-order information criterion, corrected for small sample sizes (AICc; Burnham & D.R. 2002). Models with ΔAICc values of 0-2 do have similar support then the best model, whereas those with ΔAICc > 2 have substantially lower support (Burnham & Anderson 2004). These were compared to the model for 1980 in terms of parameter estimates but its smaller sample size prevented comparisons through AICc. Standardized regression coefficients (β) were obtained in regression analyses as a measure of the sign and magnitude effects of predictor variables (i.e., analyses were carried out with standardized variables, such that their averages are 0 and variances are 1) to assess the relative importance of landscape variables in predicting species richness and habitat breadth of the community. Outliers and influential points were investigated by examining standard regression diagnostics (residual vs. prediction plot, Q-Q plots, and Cook's distance). No outlier or highly influential points were detected. The residuals of the regression models did not show a clear spatial autocorrelation pattern (tested by Moran's I statistic with inverse distance weighting and Euclidean distance calculation; Cliff & Ord 1981), except for the residuals from the regression model with species richness and landscape data of 2001 (SPP2001: $P = 0.03$; SPP1980: $P = 0.83$; SPP1956: $P = 0.62$; HB2001: $P = 0.64$; HB1980: $P = 0.90$; HB1956: $P = 0.67$). Thus, there was a lack of influence of the spatial location and proximity of the 40 landscapes on the majority of the observed patterns of variation in the response variables.

To explore the differences in the responses of individual species we modeled species that belonged to the group with high and moderate preference for extensive cereal fields and were recorded at 15-85% of landscapes (n = 26). We used generalized linear models with a logit link function (logistic regression) and compared models for 2001 and 1956 with AICc. All the statistical analyses were carried out using R software.

Results

Trajectories of change

With the exception of percentage of croplands, all other indicators of landscape change increased considerably between 1956 and 2001 (Fig. 3). In Spain, this period was characterized by the enlargement of the fields (*AP* increased by 76% on average), the dispersion of built-up areas (*DIS* increased by 23.9%), the development of linear infrastructure that strongly fragmented landscapes (S_{eff} increased by 169.8%), and a moderate decline

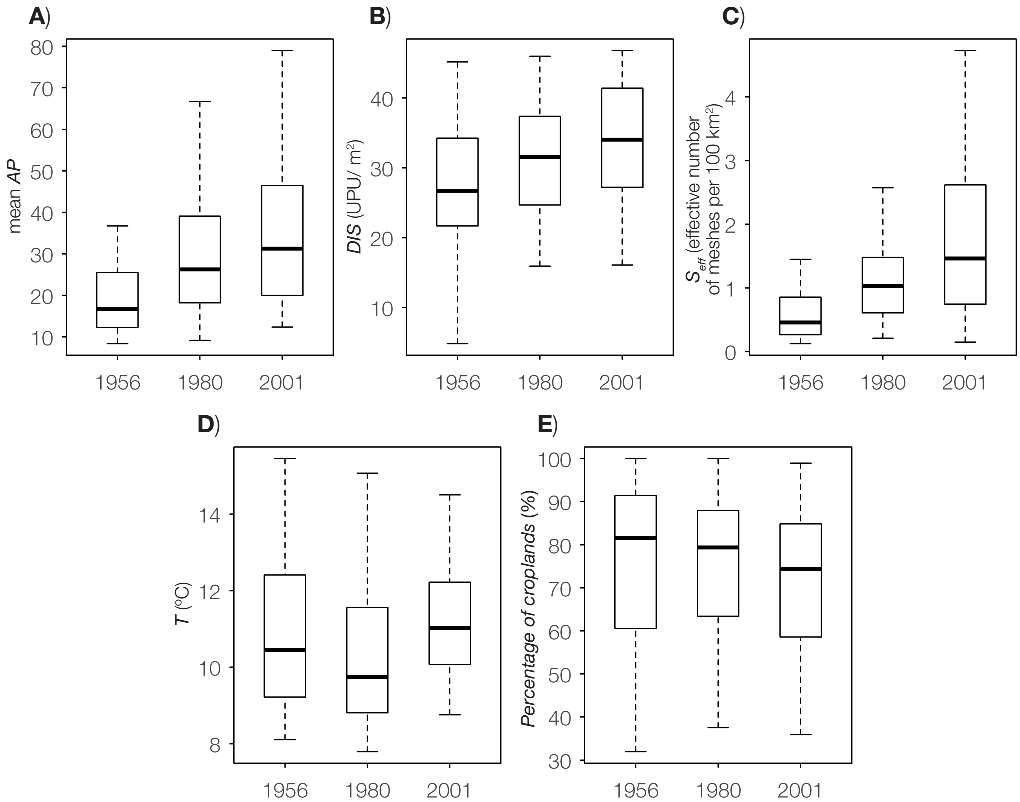

Figure 3. Box and whisker plots showing the variation of (A) farming intensity (calculated as the mean ***area-to-perimeter ratio*** of the fields, *AP*), (B) urban sprawl (calculated as the ***degree of urban dispersion***, *DIS*), (C) landscape fragmentation (calculated as the ***effective mesh density***, S_{eff}), (D) ***mean temperature*** (*T*ºC), and (E) the ***percentage of cropland*** area, from 1956 to 2001 in the sample of 40 landscape plots indicated in Figure 2 (for 1980, only data for 34 landscape plots were available). Temperatures were five-year mean values for the cells in each time step.

of the proportion of cultivated land (5.7%). In addition, mean temperature increased by 0.52 ºC.

Considering all 40 lanscapes individually, *AP* and S_{eff} increased in all of them, *DIS* increased in 93%, *T* increased in 60%, and *PC* declined in 68% of the landscapes. The rate of change varied through time periods, except for *DIS* (1980: +11.8%; 2001: +11.5%) and *PC* (1980: +3%; 2001: -3.8%). *AP* increased more in the first period (+44.2%) than in the second period (+27.6%), as well as S_{eff} (1980: +127.2%; 2001: +73.1%). On the contrary, *T* slightly declined in the first period (-5.4%) and then increased in the second period (16.1%).

Effects of environmental change on species richness

Current species richness for the bird group with high preference for extensive cereal fields was 12.5 ± 3.0 SD (range: 5-19 species), for the group of high-moderate preference was 21.4 ± 4.2 SD (range: 11-31 species), and for the group of high-moderate-low preference was 43.5 ± 9.3 SD (range: 24-60 species). Average total bird richness was 72.2 ± 18.3 SD (range: 38-110 species). Four species were present in all landscapes: the Kestrel (*Falco tinnunculus*), the Hoopoe (*Upupa epops*), the House sparrow (*Passer domesticus*), and the Common linnet (*Carduelis cannabina*). Among species with high preference for extensive cereal fields the most common and widespread species were the Red-legged partridge (*Alectoris rufa*), the Crested lark (*Galerida cristata*), and the Corn bunting (*Miliaria calandra*), present in 39 landscapes.

The model relating current species richness with past landscape and environmental predictors was the one with the highest strength of evidence in all bird groups (Fig. 4A; Table 1; Tables S4-S5). For instance, for birds with high-moderate preference for cereal fields, model weight was 1.0 and explained 42.6% of the variance in species richness. Its weight of evidence was considerably higher than that of the model considering current predictors (Wi = 0.0; R^2 = 0.133). The variance explained by the model based on predictors from 1980 was only slightly lower than the variance explained by the model based on predictors from 1956. Among all predictors, the urban sprawl showed the highest magnitude of effects throughout time, although temperature reached a slightly higher magnitude effect in 1956. Other predictors did not show any significant influence on current species richness (Fig. 4A; Table 1; Tables S4-S5).

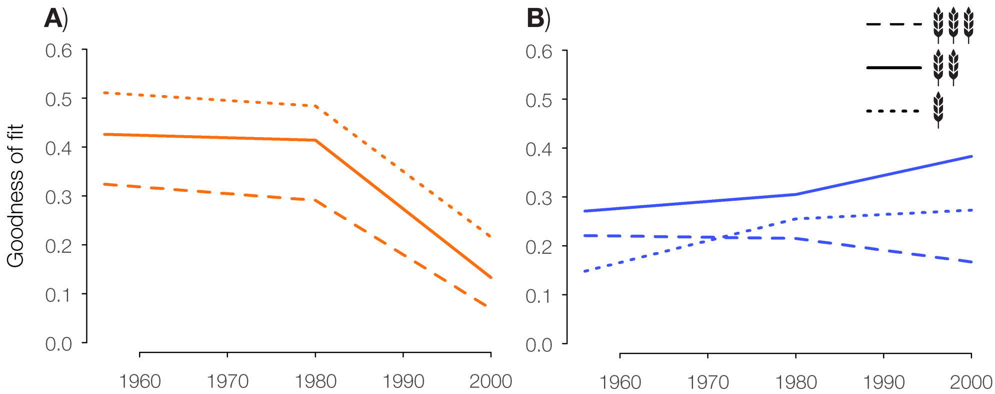

Figure 4. Variation in goodness of fit (R^2) of models for (A) current species richness and (B) median habitat breadth of the bird community, using landscape/environmental predictor variables measured at three time points for the sample of 40 landscape plots indicated in Figure 2 (for 1980, only data for 34 landscape plots were available). Models were performed for the three bird groups considered, depending on their habitat preferences for extensive cereal fields: high (three spikes), high+moderate (two spikes), and high+moderate+low (one spike; see Methods, section ***Species data*** for details).

The magnitude effect of some predictor variables changed through time. For example, current species richness was slightly negatively affected by agricultural intensification in 2001, but positively affected by agricultural intensification in 1980 and 1956 (Fig. 5; Table 1). Also, the effect of present temperature on current bird richness was positive and very weak, but past temperatures showed negative and higher effects for 1956 than for 1980 (Fig. 6; Table 1). The negative contribution of urban sprawl was highest in 1980

Table 1. Regression results for species richness of birds with high and moderate preference for extensive cereal crops during the breeding season (2001). Standardized regression coefficients (β) are shown for each landscape variable: area-perimeter ratio of the fields (*AP*), degree of urban dispersion at 2 km (DIS_2), effective mesh density (S_{eff}), mean temperature (*T*), percentage of croplands (*%C*). K: number of effects + intercept. *Wi*: model weights. AICc: AIC corrected for small sample sizes. ΔAICc = AICc – $AICc_{min}$.

		INTENSIVE FARMING	URBAN SPRAWL	LANDSCAPE FRAGMENT.	CLIMATE	AMOUNT OF CROPLANDS				
	R^2	$\beta\ AP$	$\beta\ DIS_2$	$\beta\ S_{eff}$	$\beta\ T$	β %*C*	K	W_i	AIC_c	ΔAICc
2001	0.133	-0.059	-0.235	0.004	0.043	-0.194	7	0	237.7	16.3
1980	0.414	0.158	-0.452	0.045	-0.380	-0.047				
1956	0.426	0.303	-0.443	0.123	-0.506	-0.007	7	1	221.4	0.0

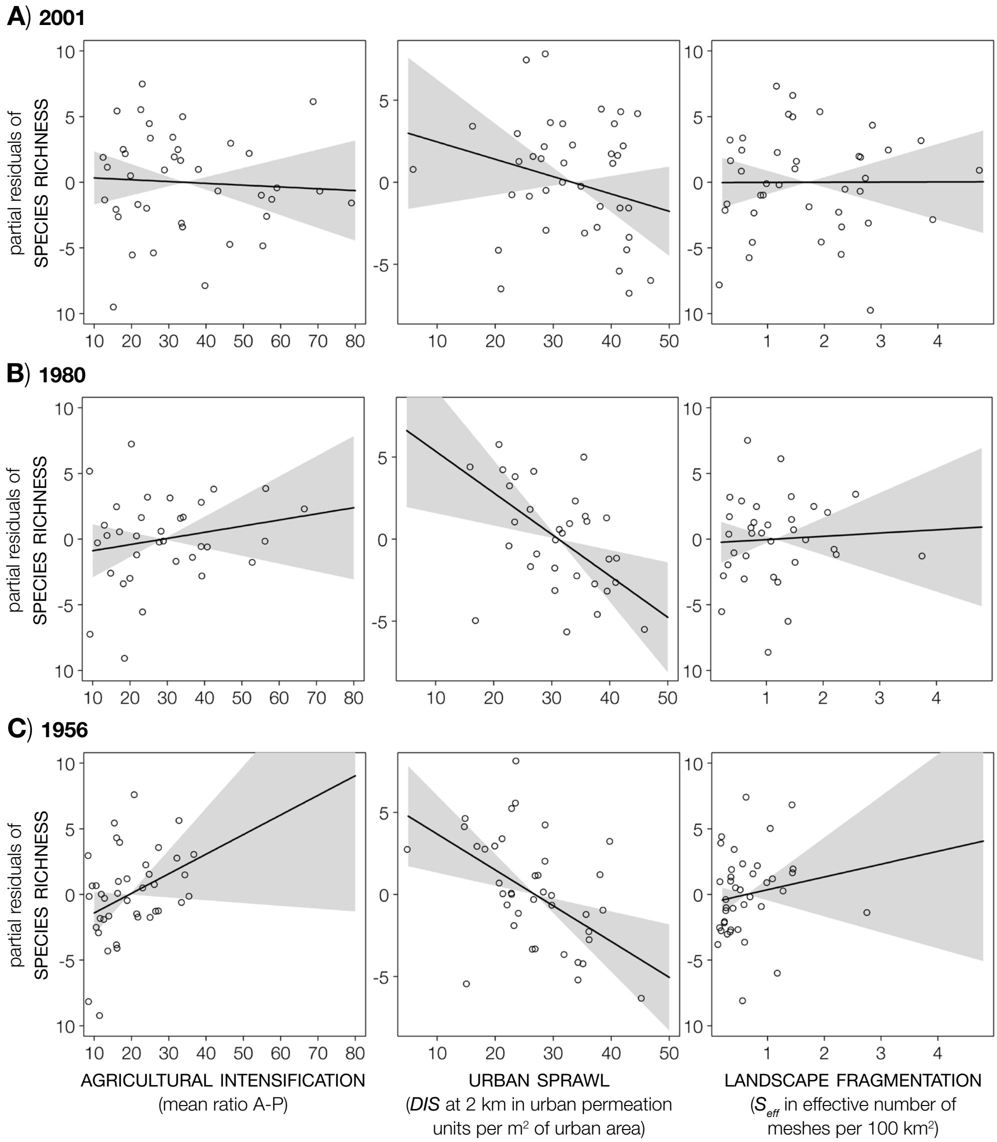

Figure 5. Partial residual plots illustrating the influence of agricultural intensification, urban sprawl, and landscape fragmentation due to infrastructure on species richness of breeding birds at present (2001), in the sample of 40 landscapes (34 for 1980), considering species with high and moderate preference for extensive cereal fields. Residuals are calculated by keeping the other predictor variables except agricultural intensification, urban sprawl, and landscape fragmentation, respectively, at their means, thus partialling out their effects.

and 1956. The effect of landscape fragmentation on species richness was very weak, though perceptible and positive for 1956. The percentage of croplands affected species richness negatively, though its contribution was only

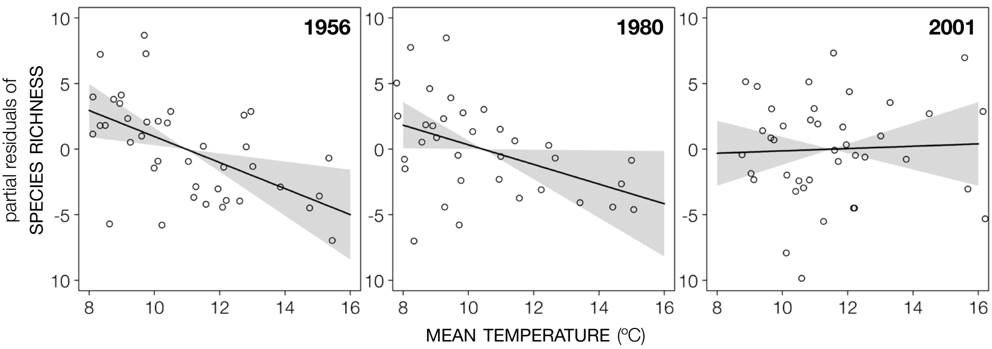

Figure 6. Partial residual plots illustrating the influence of mean temperature on species richness of breeding birds in the present (2001), in the sample of 40 landscapes (34 for 1980), considering species with high and moderate preference for extensive cereal fields. Residuals are calculated by keeping the other predictor variables except agricultural intensification, urban sprawl, and landscape fragmentation, respectively, at their means, thus partialling out their effects.

appreciable at present and for the groups with less species with preference for extensive cereal fields (SPP1,2 and SPP1,2,3; Fig. 4A; Table 1; Tables S4-S5).

Effects of environmental change on habitat breadth

The median habitat breadth of the bird community increased when species with a lower preference for extensive cereal fields were considered (HB = 0.58 ± 0.07 SD, range: 0.46-0.75, for the bird group with high preference for extensive cereal fields; 0.68 ± 0.04 SD, range: 0.57-0.77, for the group of high-moderate preference; 0.71 ± 0.02 SD, range: 0.65-0.77, for the group of high-moderate-low preference). Among species with high preference for extensive cereal fields, the highest HB corresponded to the Carrion crow (*Corvus corone*) and the Corn bunting (*Emberiza calandra*) (HB = 0.79), while the lowest HB corresponded to the Great bustard (*Otis tarda*) (HB = 0.13) and the Montagu's harrier (*Circus pygargus*) (HB = 0.14).

The models for current median habitat breadth of the bird community showed differences in the goodness of fit depending on the bird group considered (Fig. 4B; Table 2; Tables S6-S7). For SPP1 the model based on past values of the predictors was the best one, although the variance explained was low (Wi = 0.79; R^2 = 0.221). However, for SPP1,2 and SPP1,2,3 the models showing the highest goodness of fit were those based on present values of the predictors (SPP1,2: Wi = 0.97; R^2 = 0.383; SPP1,2,3: Wi = 0.96; R^2 = 0.273).

Table 2. Regression results for the median habitat breadth of the bird community during the breeding season (2001), considering birds with high and moderate preference for extensive cereal crops. Standardized regression coefficients (β) are shown for each landscape variable: area-perimeter ratio of the fields (*AP*), degree of urban dispersion at 2 km (DIS_2), effective mesh density (S_{eff}), mean temperature (*T*), percentage of croplands (*%C*). K: number of effects + intercept. *Wi*: model weights. AICc: AIC corrected for small sample sizes. ΔAICc = AICc – $AICc_{min}$.

		INTENSIVE FARMING	URBAN SPRAWL	LANDSCAPE FRAGMENT.	CLIMATE	AMOUNT OF CROPLANDS				
	R^2	$\beta\ AP$	$\beta\ DIS_2$	$\beta\ S_{eff}$	$\beta\ T$	β %C	K	W_i	AIC_c	ΔAICc
2001	0.383	-0.443	-0.030	0.390	0.053	0.266	7	0.97	-139.0	0.0
1980	0.305	-0.403	-0.119	0.370	0.053	0.270				
1956	0.271	-0.326	0.018	0.140	-0.065	0.368	7	0.03	-132.3	6.7

The predictors with a stronger influence on the current HB were agricultural intensification, landscape fragmentation and percentage of croplands (Fig. 7; Table 2). S_{eff} had a strong positive effect on HB and its influence decreased towards the past in all bird groups. The *PC* also showed a positive effect on HB and its overall influence increased towards the past. Mean *AP* was also an important predictor throughout time, but with a negative effect on present HB. However, its influence increased towards the present in groups SPP1,2 and SPP1,2,3 and increased towards the past in group SPP1. The rest of predictor variables played a minor role in determining current habitat breadth of the bird community.

Interspecific variation in the response to changing landscape and environment

There was a reduced interspecific variation in results of the models for 1956 and 2001. Models performed with predictor variables from 1956 had the highest strength of evidence in seventeen species (Table 3), with the predictive power ranging between 0.171 for the European roller (*Coracias garrulus*), and 0.654 for the Ortolan bunting (*Emberiza hortulana*). Models performed with predictor variables from 2001 had the highest strength of evidence only in two species, the Stock dove (*Columba oenas*) and the Thekla lark (*Galerida theklae*), for which the variance explained was, respectively 0.313 and 0.137. For seven species there were not clear differences between models performed for these two periods. Yet, for two of them – Rock bunting (*Emberiza cia*) and

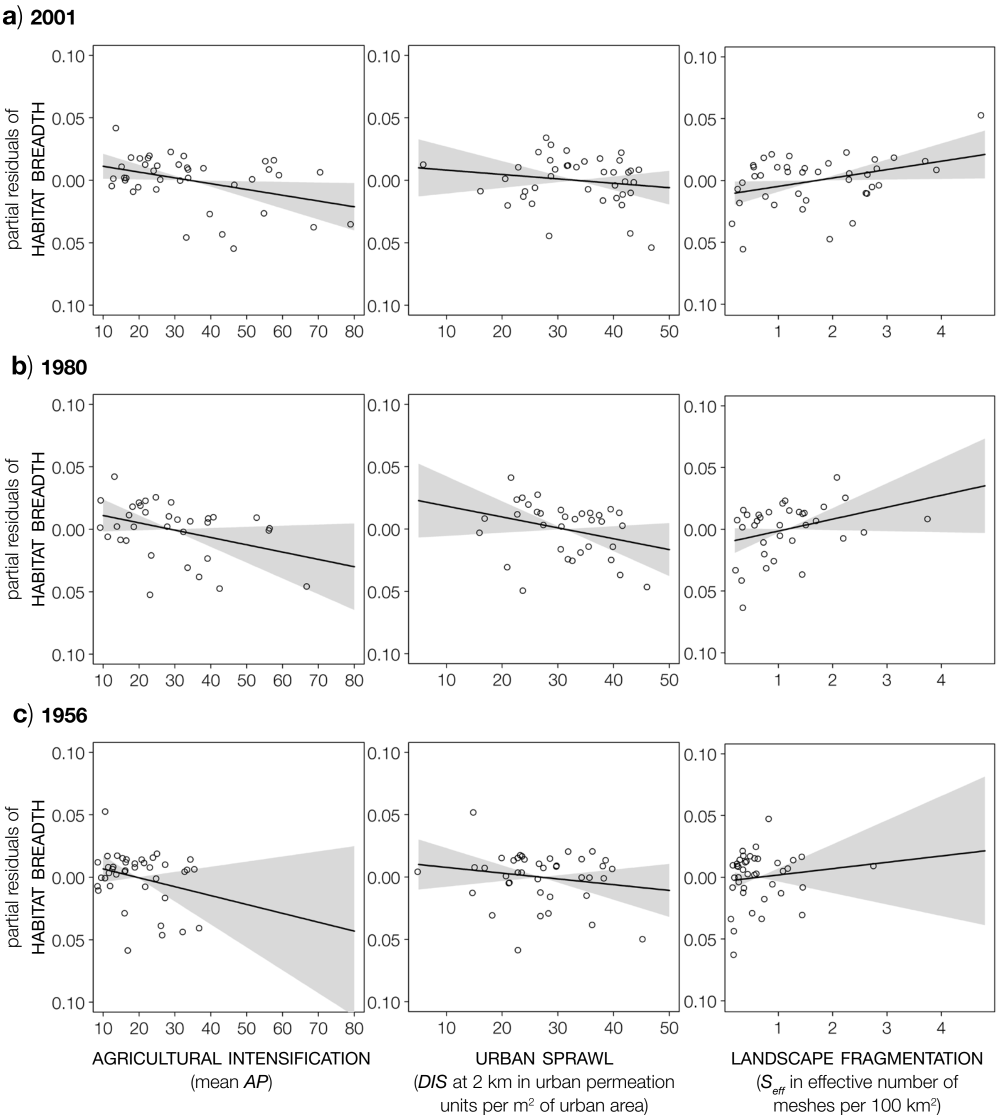

Figure 7. Partial residual plots illustrating the influence of agricultural intensification, urban sprawl, and landscape fragmentation due to infrastructure on the median habitat breadth of the bird community at present (2001), in the sample of 40 landscapes (34 for 1980), considering species with high and moderate preference for extensive cereal fields. Residuals are calculated by keeping the other predictor variables except agricultural intensification, urban sprawl, and landscape fragmentation, respectively, at their means, thus partialling out their effects.

Spotted flycatcher (*Muscicapa striata*) – the models performed with predictor variables from 1980 were clearly more explicative than the one with predictor variables from 2001 (0.138 vs. 0.247 and 0.054 vs. 0.241 respectively).

Table 3. Results of models built for presence/absence of each individual species and predictor variables in 2001, 1980, and 1956. K: number of effects + intercept. *Wi*: model weights. AICc: AIC corrected for small sample sizes. ΔAICc = AICc – $AICc_{min}$. In bold type, species exhibiting a time-lag response.

SCIENTIFIC NAME	TIME	DEVIANCE EXPLAINED	*K*	*Wi*	AICc	ΔAICc
Alauda arvensis	2001	0.033	6	0.0	65.7	21.9
	1980	0.398				
	1956	0.447	6	1.0	43.8	0.0
Buteo buteo	2001	0.112	6	0.43	60.5	0.5
	1980	0.096				
	1956	0.123	6	0.57	60.0	0.0
Calandrella brachydactyla	2001	0.166	6	0.17	52.0	3.2
	1980	0.399				
	1956	0.238	6	0.83	48.8	0.0
Circus cyaneus	2001	0.159	6	0.44	48.2	0.5
	1980	0.135				
	1956	0.172	6	0.56	47.7	0.0
Circus pygargus	2001	0.182	6	0.45	44.9	0.4
	1980	0.206				
	1956	0.193	6	0.55	44.5	0.0
Cisticola juncidis	2001	0.248	6	0.13	55.0	3.8
	1980	0.281				
	1956	0.318	6	0.87	51.3	0.0
Columba oenas	2001	0.313	6	0.94	52.0	0.0
	1980	0.224				
	1956	0.211	6	0.06	57.6	5.6
Coracias garrulus	2001	0.089	6	0.27	55.5	2.0
	1980	0.171				
	1956	0.134	6	0.73	53.5	0.0
Corvus corax	2001	0.197	6	0.24	56.1	2.2
	1980	0.259				
	1956	0.241	6	0.76	53.9	0.0
Corvus corone	2001	0.153	6	0.0	56.0	10.7
	1980	0.568				
	1956	0.371	6	1.0	45.3	0.0
Emberiza cia	2001	0.138	6	0.30	60.9	1.7
	1980	0.247				
	1956	0.170	6	0.70	59.3	0.0
Emberiza hortulana	2001	0.225	6	0.0	47.6	18.3
	1980	0.680				
	1956	0.654	6	1.0	29.3	0.0
Falco naumanni	2001	0.128	6	0.51	60.7	0.0
	1980	0.079				
	1956	0.128	6	0.49	60.7	0.0

Falco subbuteo	2001	0.082	6	0.01	62.1	9.0
	1980	0.132				
	1956	0.257	6	0.99	53.0	0.0
Fringilla coelebs	2001	0.233	6	0.12	50.6	3.9
	1980	0.309				
	1956	0.317	6	0.88	46.7	0.0
Galerida theklae	2001	0.137	6	0.84	51.3	0.0
	1980	0.136				
	1956	0.060	6	0.16	54.6	3.3
Hirundo daurica	2001	0.132	6	0.0	53.6	14.7
	1980	0.602				
	1956	0.458	6	1.0	38.9	0.0
Motacilla cinerea	2001	0.053	6	0.10	49.7	4.5
	1980	0.049				
	1956	0.174	6	0.90	45.2	0.0
Muscicapa striata	2001	0.054	6	0.66	57.1	0.0
	1980	0.241				
	1956	0.024	6	0.34	58.8	1.4
Oenanthe oenanthe	2001	0.072	6	0.0	62.6	14.8
	1980	0.358				
	1956	0.357	6	1.0	47.9	0.0
Otis tarda	2001	0.088	6	0.05	60.6	5.8
	1980	0.229				
	1956	0.203	6	0.95	54.7	0.0
Petronia petronia	2001	0.155	6	0.42	52.6	0.7
	1980	0.194				
	1956	0.170	6	0.58	51.9	0.0
Phylloscopus bonelli	2001	0.190	6	0.0	58.7	13.3
	1980	0.387				
	1956	0.433	6	1.0	45.5	0.0
Pterocles alchata	2001	0.264	6	0.0	44.0	13.6
	1980	0.317				
	1956	0.604	6	1.0	30.4	0.0
Pterocles orientalis	2001	0.193	6	0.05	58.6	5.7
	1980	0.154				
	1956	0.298	6	0.95	52.8	0.0
Tetrax tetrax	2001	0.054	6	0.04	66.6	6.2
	1980	0.076				
	1956	0.166	6	0.96	60.5	0.0

Discussion

Evidence of time-lag responses

Our results clearly indicate that the bird community of agricultural landscapes responds to human-induced changes with a significant time-lag, and that this time-lag mostly, but not exclusively affects typical steppe birds, i.e. those with higher preference for extensive cereal crops. This delayed response was also supported by a more detailed analysis at the species level, where only two species exhibited a stronger goodness of fit with present-day predictors. In general, these results suggest that current species diversity is not in equilibrium with contemporary landscape structure and climate. This time-lag suggests the existence of a substantial extinction debt (Kuussaari et al. 2009), which can induce future shifts in the structure of the farmland bird community. Most studies reporting time-lagged species responses are mainly limited to plants (e.g., Lindborg & Eriksson 2004; Helm et al. 2006) and at the scale of habitat patches (Kuussaari et al. 2009; Krauss et al. 2010). There are a few studies reporting time-lagged responses in birds, mostly in wooded areas and in relation to deforestation (Brooks et al. 1999; Brook et al. 2003; Metzger et al. 2009). This is the first study revealing time-lagged responses in the bird communities of Mediterranean agricultural landscapes.

In our case study, the precise time frame of such time-lag is not clear, but might vary between 20 and 40 years. Most models based on past values of landscape predictors explained more variance and performed better than models using present-day predictors. The differences between models with predictors from 1956 and 1980 were relatively small, even though most changes in the landscapes took place between these two dates (1956-1980).

Time-lagged responses and extinction debts might be more common than previously acknowledged, and could perhaps be the rule across a wide range of taxa and ecosystems. Such delayed responses really pose a challenge for biodiversity conservation. Predictions from models performed with both present characteristics of the habitats and species information can lead to incorrect conclusions (e.g., Vallecillo et al. 2009). The present study also warns about the dangers of projecting species distribution models onto future conditions if current species abundances and distributions are not in equilibrium with contemporary environmental conditions and if processes behind species distribution dynamics are not explicitly included.

Relative contribution of the drivers of landscape change

To our knowledge, this is the first study assessing the relative and independent effects of several landscape factors commonly recognized as contributing to bird declines in agricultural landscapes. Our results suggest a prominent role of urban sprawl and climate in shaping current species richness of the bird community breeding in farmlands. Those landscapes that 50 years ago had a lower degree of urban sprawl and a lower mean temperature exhibit now higher species richness. However, these two factors did not show any influence on the variations in the degree of specialization of the bird community, which was mainly shaped by landscape fragmentation and agricultural intensification.

Accumulating evidence suggests that agricultural intensification is the main driver of species loss in farmlands (Donald et al. 2001). However, our results do not show that agricultural intensification was the primary factor influencing species richness at the landscape scale. Regarding the percentage of croplands, and based on its small contribution to the models, we may conclude that there is no clear influence of the variation in the amount of cultivated land throughout landscapes and time on the observed responses to agricultural intensification, urban sprawl and climate. Various agricultural management factors have changed simultaneously, tuning agricultural intensification into a multivariate process whose components are difficult to disentangle (Chamberlain et al. 2000). Mean field size (or the *AP*) and the percentage of croplands are two of the most important variables describing agro-systems (Geiger et al. 2010; Fritz et al. 2015), and both are critical inputs to agricultural monitoring (Fritz et al. 2015). We consider that by using these two metrics we were able to quantify the landscape simplification derived from agricultural intensification. The effects of agricultural intensification have been mostly studied at microhabitat and field scales, but scaling-up results of field experiments to larger scales may not be appropriate, since it is widely contended that processes operating at local scales do not have a similar dominant role at regional or macroecological scales (Tscharntke et al. 2005; Concepción et al. 2008). Therefore, the lessons from those studies may then lead to suboptimal or insufficient management practices when they have to be applied at the landscape planning scale (Concepción & Díaz 2011).

It is true that past agricultural intensification had a positive effect on current species richness, but compared to other predictors this effect was relatively weak. The levels of AP in 1956 were overall very low, so this effect is consistent with the conclusions of previous studies suggesting that in extensive farmlands certain landscape changes associated with intensification (e.g., increased productivity) may have positive effects on species richness and abundance (Tscharntke et al. 2005; Wretenberg et al. 2007; Wretenberg et al. 2010). However, our results show that this positive influence disappeared between 1956 and 2001.

Agricultural intensification had a strong influence in the habitat breadth of the bird communities of agricultural landscapes. Where agricultural intensification increased, the average habitat breadth of the species that make up the bird community became lower, i.e. the proportion of habitat specialist species became higher. This contrasts with the reported declining trends for specialist farmland birds in other regions like countries like UK (Siriwardena et al. 1998) or France (Julliard et al. 2004). Yet, habitat breadth is only marginally related to population trends in Spain (Seoane & Carrascal 2008). Previous studies showed that functional diversity of farmland bird communities was negatively affected by agricultural intensification (Guerrero et al. 2011), but the level of habitat specialization of the bird communities was not assessed. In other cases, it has been suggested that intensified agriculture can lead to biotic homogenization by increased cover of cultivated land, i.e., by agricultural expansion (Dormann et al. 2007; Flynn et al. 2009; Kleijn et al. 2009), which is consistent with the detected positive influence of percentage of croplands on the habitat breadth of the bird communities.

Among the landscape predictors considered, urban sprawl showed the strongest influence on species richness. This is supported by previous studies with farmland birds that reported a negative influence of both density and proximity to roads, buildings, and villages (Osborne et al. 2001; Silva et al. 2004). Interestingly, we found a fifty-years delayed effect of urban sprawl, which contrasts with the common belief that urban sprawl affects biodiversity when it refers to cities and largely urbanized areas. The spatial arrangement of built-up areas, which might be related to improved accessibility and then hunting and other disturbances, seems to play a fundamental role in this cause-effect relationship.

We did not find a significant influence of landscape fragmentation due to transport infrastructure over the species richness but it strongly influenced the current habitat breadth of the bird community. More fragmented landscapes presented higher values of habitat breadth, i.e., a higher proportion of habitat generalist species. The detrimental effect of landscape fragmentation has been previously documented particularly for habitat specialists (Devictor et al. 2008b; Reino et al. 2013), which might be negatively affected by increased edge densities and number of patches. Our results support the view that more attention should be given to the incorporation of fragmentation metrics on the monitoring of agricultural landscapes.

Relative contribution of climate change

Not only landscape has changed during the last decades, global warming has increased global temperatures by 0.7 degrees since the beginning of the 20th century and temperatures are still rising (IPCC 2007). The average increase in mean temperature found for this study area and study period is consistent with this global warming, as well as with increasing trends in temperature previously reported for Spain (de Castro et al. 2005). The relationship between present species richness and mean temperature was clearly stronger when we used temperature measured in 1956, irrespective of the habitat variables, indicating that bird species are affected by climate and that warming is driving bird diversity out of equilibrium. Lags in the response to changing environment have been detected in both plants and animals (e.g., Weimerskirch et al. 2003; Wu et al. 2015), ranging between a few months and some years (Weimerskirch et al. 2003), up to several decades (Brooks et al. 1999). Devictor et al. (2012) showed that European birds have a climatic lag of 212 km northwards between 1990 and 2008. Our results suggest that the lag could be even greater as the model for 1980 already shows a decrease in the adjustment between species richness and temperature. The reason for this climatic debt is something worth further research. Since birds are among the most mobile animals, they should in principle have little problem finding new suitable habitats and they are expected to track climate change more closely (Araújo & Pearson 2005). Nevertheless, many bird species show strong philopatry, returning to breed to their natal areas (e.g., the great bustard; Alonso et al. 1998; Martín et al. 2008). A strong attachment to an area combined with high thermal resilience could keep a population out of their climatic optimum for a long time.

The negative influence of mean temperature on species richness could be related to summer residence and the prevention of high temperature and water stress in the warmest season (Williams & Tieleman 2000; Tieleman et al. 2002). In addition, our results are consistent with other studies developed at species level, for example with the Calandra lark, for which probability of occurrence declines with mean annual temperature (Reino et al. 2013). Moreover, there is a great deal of evidence of the influence of recent temperature increase on the breeding biology of many bird species, both at local and large spatial scales (Visser 2008). Therefore, we postulate an impoverishment of breeding bird communities of agricultural landscape if mean temperatures continue to increase in the future (IPCC 2007; Brunet 2009). Our work indicates that climate change adds to agricultural intensification and other factors accounting for landscape degradation in threatening agricultural bird communities.

Conclusions

The changes in landscape structure and the warming climate over the past half century are influencing the present-day species richness of the bird community in Mediterranean agricultural landscapes. We found strong evidence of time-lagged responses of birds to well-known drivers of global change. Time-lagged responses to landscape changes are rarely considered in management plans (Kuussaari et al. 2009). Conservation decisions based on the analysis of how species respond to present-day landscapes are likely insufficient to prevent species losses in the future. Extinction debt is likely to come due unless we better manage agricultural landscapes to prevent extinctions (which are currently debts) from occurring. Hence, landscapes with high imprint of urban sprawl and other pressures become challenges for conservation planning to prevent further impacts, reinforce remnant populations, and restore vital ecological interactions and processes.

The interactions between human activities and natural processes shape farmland ecosystems, resulting in complex multifunctional landscapes (Fahrig et al. 2011). We showed that the structure of the bird community of these areas is the result of multiple interacting drivers of landscape and environmental change, which operates along different dimensions. We revealed that urban sprawl and climate play a greater role than agricultural intensification in explaining landscape-scale values of species richness in agricultural areas, whereas landscape fragmentation and agricultural intensification play a prominent role in determining the level of specialization of the bird community. Therefore, the declining trends of birds of agricultural landscapes should be viewed as the result of a complex combination of processes acting at different spatial and temporal scales.

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Supplementary information

Table S1. Web Map Services
Table S2. List of the 14 major habitat types considered in this study.
Table S3. List of the bird species considered in this study.
Tables S4-7. Regression results for bird groups with high (SPP1) and high+-moderate+low preference for extensive cereal fields (SPP1,2,3).
Figure S1. Partial residual plots illustrating the influence of percentage of croplands on species richness of breeding birds at present time (2001).
Figure S2. Partial residual plots illustrating the influence of mean temperature on the median habitat breadth of the bird community at present time (2001).
Figure S3. Partial residual plots illustrating the influence of percentage of croplands on the median habitat breadth of the bird community at present time (2001).

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Table S1. Orthoimages used for the digitalization, available via Web Map Services (WMS).

Region	Time	Orthoimage	Source	Scale (resolution)
Andalucía	2009	2008-2009	REDIAM[1]	1:5,000 (50 cm)
	2000	2001-2002	REDIAM	1:10,000 (50 cm)
	1980	1977-1980	REDIAM	1:5,000 (50 cm)
	1956	1956-1957	REDIAM	1:10,000 (1 m)
Aragón	2009	2009	IDEARAGON[2]	1:5,000 (50 cm)
	2000	1997-2000	IDEARAGON	1:5,000 (50 cm)
	1980	-	-	-
	1956	1956	IDEARAGON	1:5,000 (50 cm)
Castilla-León	2009	2009-2010	ITACYL[3]	1:5,000 (25 cm)
	2000	1999-2002	ITACYL	1:5,000 (25 cm)
	1980	1977-1983	ITACYL	1:5,000 (50 cm)
	1956	1956-1957	ITACYL	1:5,000 (40 cm)
Catalonia	2009	2009	ICGC[4]	1:5,000 (50 cm)
	2000	2001	ICGC	1:5,000 (50 cm)
	1980	1986-1987	ICGC	1:5,000 (50 cm)
	1956	1956	ICGC	1:5,000 (50 cm)
Extremadura	2009	2008	IdeExtremadura[5]	1:5,000 (50 cm)
	2000	1998-2002	IdeExtremadura	1:5,000 (50 cm)
	1980	-	-	-
	1956	1956	IdeExtremadura	1:5,000 (50 cm)
Galicia	2009	2009	Información Xeográfica de Galicia	1:5,000 (25cm)
	2000	2002-2003	Información Xeográfica de Galicia	1:5,000 (50 cm)
	1980	-	-	-
	1956	1956-1957	Información Xeográfica de Galicia	1:10,000 (1m)
Madrid	2009	2009	IDEM[6]	1:5,000 (50 cm)
	2000	2001	IDEM	1:5,000 (30 cm)
	1980	1975	IDEM	1:5,000 (50 cm)
	1956	1956	IDEM	1:5,000 (1 m)
Murcia	2009	2009	IDERM[7]	1:5,000 (50 cm)
	2000	2002	IDERM	1:5,000 (50 cm)
	1980	1981	IDERM	1:5,000 (50 cm)
	1956	1956	IDERM	1:5,000 (50 cm)
Navarra	2009	2009	SITNA[8]	1:5,000 (50 cm)
	2000	1998-2000	SITNA	1:5,000 (50 cm)
	1980	-	-	-
	1956	1956	SITNA	1:10,000 (1m)

[1] Red de información ambiental de Andalucía
[2] Infraestructura de datos espaciales de Aragón
[3] Instituto Tecnológico Agrario. Junta de Castilla y León
[4] Institute Cartogràfic i Geològic de Catalunya
[5] Infraestructura de datos espaciales de Extremadura
[6] Infraestructura de datos espaciales de la Comunidad de Madrid
[7] Infraestructura de datos espaciales de referencia de la región de Murcia
[8] Sistema de Información Territorial de Navarra

Table S2. List of the 14 major habitats from Carrascal & Palomino (2008) considered in this study to calculate the habitat breadth of the bird community.

SPANISH NAME	ENGLISH NAME
Mosaicos agropecuarios	Complex agricultural mosaics
Cultivos herbaceous extensivos de secano	Dry extensive cereal fields
Cultivos extensivos de regadío	Irrigated cereal fields
Viñedos	Vineyards
Olivares y frutales	Olive groves and fruit trees
Ambientes urbanizados	Urban environments
Herbazales y prados	Herbaceous habitats
Humedales	Freshwater marshlands
Matorrales	Scrublands
Enebrales y sabinares	Open juniper woodlands and scrublands
Encinares y alcornocales	Sclerophyllous woodlands
Pinares	Pinewood forests
Riberas arboladas	Riverbank copses
Bosques deciduos	Deciduous forests

Table S3. List of bird species considered in the study, grouped according to their habitat preference for extensive cereal fields.

BIRD GROUP			SCIENTIFIC NAME	ENGLISH NAME
1,2,3	**1,2**	**1**	*Alauda arvensis*	Sky lark
high+	high+	high	*Alectoris rufa*	Red-legged partridge
medium+	medium		*Calandrella brachydactyla*	Short-toed lark
low			*Circus cyaneus*	Hen harrier
n = 75	n = 39	n = 22	*Circus pygargus*	Montagu's harrier
(39 + 36)	(22 + 17)		*Cisticola juncidis*	Fan-tailed warbler
			Columba oenas	Stock dove
			Corvus corone	Carrion crow
			Corvus corax	Raven
			Coturnix coturnix	Quail
			Miliaria calandra	Corn bunting
			Emberiza cia	Rock bunting
			Emberiza hortulana	Ortolan bunting
			Falco naumanni	Lesser kestrel
			Falco subbuteo	Eurasian hobby
			Galerida cristata	Crested lark
			Melanocorypha calandra	Calandra lark
			Otis tarda	Great bustard
			Passer hispaniolensis	Spanish sparrow
			Pterocles alchata	Pin-tailed sandgrouse
			Pterocles orientalis	Black-bellied sandgrouse
			Tetrax tetrax	Little bustard
			Buteo buteo	Common buzzard
			Carduelis carduelis	European goldfinch
			Coracias garrulus	European roller
			Elanus caeruleus	Black-windeg kite
			Falco tinnunculus	Kestrel
			Fringilla coelebs	Eurasian chaffinch
			Galerida theklae	Thekla lark
			Hirundo daurica	Red-rumped swallow
			Lanius collurio	Red-backed shrike
			Motacilla cinerea	Grey wagtail
			Muscicapa striata	Spotted flycatcher
			Oenanthe oenanthe	Northern weather
			Petronia petronia	Rock sparrow
			Phylloscopus bonelli	Western Bonelli's warbler
			Saxicola torquata	Stonechat
			Sturnus vulgaris	Starling
			Turdus merula	Eurasian Blackbird
			Anthus campestris	Tawny pipit
			Anthus trivialis	Tree pipit

Apus apus	Common swift
Burhinus oedicnemus	Stone Curlew
Carduelis cannabina	Eurasian Linnet
Carduelis chloris	European Greenfinch
Columba livia	Rock dove
Columba palumbus	Common Wood-pigeon
Cuculus canorus	Common Cuckoo
Dendrocopos major	Great-spotted woodpecker
Emberiza cirlus	Cirl bunting
Erithacus rubecula	Robin
Hieraaetus pennatus	Booted Eagle
Hippolais polyglotta	Melodious Warbler
Hirundo rustica	Swallow
Luscinia megarhynchos	Common Nightingale
Merops apiaster	European bee-eater
Milvus migrans	Black kite
Milvus milvus	Red kite
Motacilla flava	Yellow wagtail
Oenanthe hispanica	Black-eared wheatear
Oriolus oriolus	Eurasian Golden Oriole
Parus major	Great Tit
Passer montanus	Tree sparrow
Phylloscopus collybita	Common Chiffchaff
Pica pica	Black-billed Magpie
Picus viridis	Eurasian Green Woodpecker
Saxicola rubetra	Winchat
Sitta europaea	Eurasian nuthatch
Streptopelia turtur	European Turtle-dove
Sturnus unicolor	Spotless starling
Sylvia atricapilla	Eurasian Blackcap
Sylvia borin	Garden Warbler
Sylvia cantillans	Subalpine Warbler
Upupa epops	Hoopoe
Vanellus vanellus	Lapwing

Table S4. Regression results for species richness of birds with high preference for extensive cereal crops during the breeding season (2001). Standardized regression coefficients (β) are shown for each landscape variable: area-perimeter ratio of the fields (*AP*), degree of urban dispersion at 2 km (DIS_2), effective mesh density (S_{eff}), mean temperature (*T*), percentage of croplands (*%C*). K: number of effects + intercept. W_i: model weights. AICc: AIC corrected for small sample sizes. ΔAICc = AICc – $AICc_{min}$.

		INTENSIVE FARMING	URBAN SPRAWL	LANDSCAPE FRAGMENT.	CLIMATE	AMOUNT OF CROPLANDS				
	R^2	$\beta\ AP$	$\beta\ DIS_2$	$\beta\ S_{eff}$	$\beta\ T$	$\beta\ \%C$	K	W_i	AIC_c	ΔAICc
2001	0.069	-0.009	-0.232	-0.059	-0.001	-0.020	7	0	214.9	12.8
1980	0.291	0.167	-0.413	0.046	-0.337	0.097				
1956	0.324	0.447	-0.449	0.108	-0.396	-0.027	7	1	202.1	0.0

Table S5. Regression results for species richness of birds with high, moderate, and low preference for extensive cereal crops during the breeding season (2001). Standardized regression coefficients (β) are shown for each landscape variable: area-perimeter ratio of the fields (*AP*), degree of urban dispersion at 2 km (DIS_2), effective mesh density (S_{eff}), mean temperature (*T*), percentage of croplands (*%C*). K: number of effects + intercept. W_i: model weights. AICc: AIC corrected for small sample sizes. ΔAICc = AICc – $AICc_{min}$.

		INTENSIVE FARMING	URBAN SPRAWL	LANDSCAPE FRAGMENT.	CLIMATE	AMOUNT OF CROPLANDS				
	R^2	$\beta\ AP$	$\beta\ DIS_2$	$\beta\ S_{eff}$	$\beta\ T$	$\beta\ \%C$	K	W_i	AIC_c	ΔAICc
2001	0.216	-0.035	-0.224	0.131	0.119	-0.346	7	0	298.5	18.9
1980	0.484	0.158	-0.445	0.132	-0.352	-0.201				
1956	0.511	0.188	-0.362	0.228	-0.561	-0.019	7	1	279.6	0.0

Table S6. Regression results for the median habitat breadth of the bird community during the breeding season (2001), considering birds with high preference for extensive cereal crops. Standardized regression coefficients (β) are shown for each landscape variable: area-perimeter ratio of the fields (*AP*), degree of urban dispersion at 2 km (DIS_2), effective mesh density (S_{eff}), mean temperature (*T*), percentage of croplands (*%C*). K: number of effects + intercept. W_i: model weights. AICc: AIC corrected for small sample sizes. ΔAICc = AICc – $AICc_{min}$.

		INTENSIVE FARMING	URBAN SPRAWL	LANDSCAPE FRAGMENT.	CLIMATE	AMOUNT OF CROPLANDS				
	R^2	β *AP*	β DIS_2	β S_{eff}	β *T*	β *%C*	K	W_i	AIC_c	ΔAICc
2001	0.167	-0.241	-0.005	0.301	-0.033	0.157	7	0.21	-92.2	2.7
1980	0.215	-0.364	-0.199	0.253	0.302	0.187				
1956	0.221	-0.438	0.025	0.193	0.273	0.257	7	0.79	-94.9	0.0

Table S7. Regression results for the median habitat breadth of the bird community during the breeding season (2001), considering birds with high, moderate, and low preference for extensive cereal crops. Standardized regression coefficients (β) are shown for each landscape variable: area-perimeter ratio of the fields (*AP*), degree of urban dispersion at 2 km (DIS_2), effective mesh density (S_{eff}), mean temperature (*T*), percentage of croplands (*%C*). K: number of effects + intercept. W_i: model weights. AICc: AIC corrected for small sample sizes. ΔAICc = AICc – $AICc_{min}$.

		INTENSIVE FARMING	URBAN SPRAWL	LANDSCAPE FRAGMENT.	CLIMATE	AMOUNT OF CROPLANDS				
	R^2	β *AP*	β DIS_2	β S_{eff}	β *T*	β *%C*	K	W_i	AIC_c	ΔAICc
2001	0.273	-0.366	-0.145	0.341	-0.035	0.167	7	0.96	-186.9	0.0
1980	0.255	-0.351	-0.277	0.310	0.132	0.147	7			
1956	0.148	-0.266	-0.173	0.119	0.063	0.172	7	0.04	-180.5	6.4

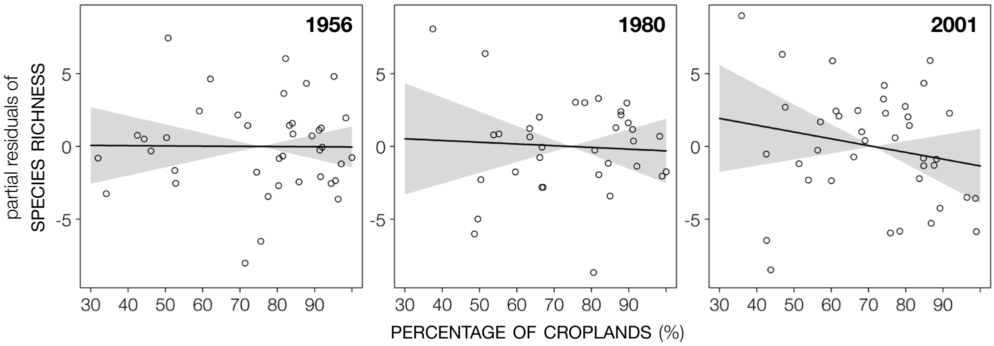

Figure S1. Partial residual plots illustrating the influence of percentage of croplands on species richness of breeding birds at present time (2001).

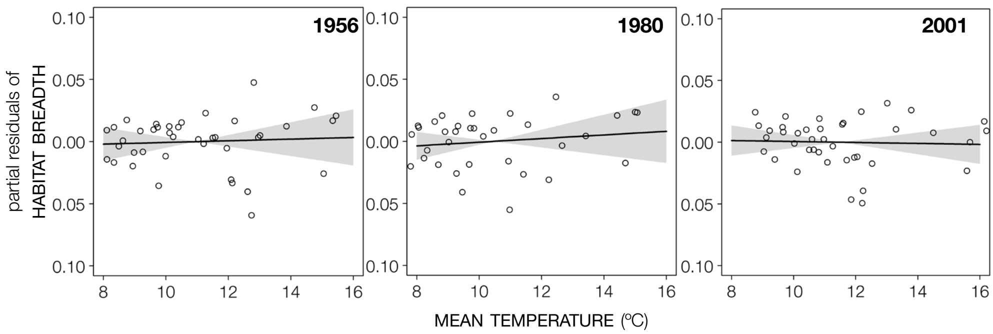

Figure S2. Partial residual plots illustrating the influence of mean temperature on the median habitat breadth of the bird community at present time (2001).

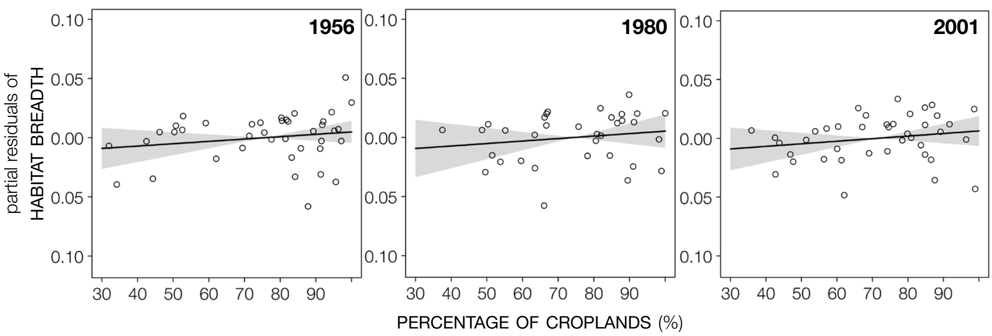

Figure S3. Partial residual plots illustrating the influence of percentage of croplands on the median habitat breadth of the bird community at present time (2001).

General synthesis & Perspectives

Síntesis general y perspectivas

Síntesis general

A continuación se presenta una integración de los principales resultados obtenidos en esta tesis doctoral, su interpretación a la luz de la literatura científica relacionada y sus implicaciones para la gestión y la conservación. Después se esbozan algunas de las líneas de trabajo que podrían abordarse en el futuro. Por último, se incluyen las conclusiones, en español y en inglés, de la tesis doctoral.

Entre la necesidad de estudios de alta potencia inferencial y la urgencia del desarrollo imparable

Trabajos recientes de síntesis destacan la necesidad de proporcionar estudios con alta potencia inferencial, mediante la aplicación de diseños Antes-Durante-Después-Impacto-Control (generalmente llamados BACI), o aproximaciones multi-escalares para tener un mayor impacto en la gestión (Roedenbeck et al. 2007; Balkenhol & Waits 2009; Lesbarrères & Fahrig 2012). En el Capítulo 1 de esta tesis se presenta un caso de aplicación de diseños (i) Antes-Durante-Después para evaluar cómo afecta la construcción de una autovía de gran capacidad al uso del espacio de los bandos de Avutarda común en el entorno de la autovía; y (ii) Antes-Durante-Después-Control-Impacto para investigar los efectos de dicha infraestructura en las tendencias poblacionales y la productividad de la población de avutarda. A día de hoy, este estudio sigue siendo uno de los pocos ejemplos de aplicación de diseños BACI en ecología de carreteras para evaluar los efectos de la construcción de vías de comunicación en medios terrestres. No obstante, sí ha sido empleado para evaluar los efectos del ruido en "carreteras fantasma" (McClure et al. 2013) o para evaluar la eficacia de medias correctoras (e.g., Soanes et al. 2013).

Igualmente, en el Capítulo 3 se aborda la interacción entre patrones de fragmentación de paisaje por infraestructuras y patrones de dispersión urbanística mediante una aproximación multi-escalar, por dos motivos. El primero es que distintos componentes de la escala pueden afectar de forma diferente a los patrones observados (Wu et al. 2006). En nuestro caso la resolución de la información de zonas construidas es clave para poder medir la dispersión urbanística (Irwin & Bockstael 2007); por tanto, hemos optado por la mayor resolución disponible y la hemos mantenido constante en todos los modelos. Sin embargo, sí hemos optado por distintas configuraciones y niveles jerárquicos. El segundo motivo es que este tipo de patrones suelen medirse y proporcionarse a distintas escalas en función de los objetivos o de la disciplina de trabajo. Así, en modelos de distribución de especies suelen utilizarse celdas UTM de 10x10 km (e.g., Reino et al. 2013); en sistemas de seguimiento los resultados suelen proporcionarse a escalas administrativas (e.g., Tzanopoulos et al. 2013); mientras que otras evaluaciones de impacto se refieren a cuencas hidrográficas o unidades de paisaje (Girvetz et al. 2008). Por tanto, esta aproximación ha permitido mejorar la interpretación y la potencia de los resultados, e incrementar la aplicabilidad de los patrones de fragmentación de paisaje y dispersión urbanística.

La mayor parte del desarrollo urbano y más de un tercio de la infraestructuras de transporte que se espera estén construidas en 2050 todavía no lo están (Seto et al. 2012; Dulac 2013). Desgraciadamente, en este momento son pocos, y referidos a un número reducido de especies, los trabajos que evalúan los efectos de estas estructuras con alta potencia inferencial (Lesbarrères & Fahrig 2012). Además, a medida que la construcción de infraestructuras progrese será cada vez más difícil cuantificar sus efectos en las poblaciones de fauna. De hecho, en el Capítulo 2 se demuestra que la omnipresencia de infraestructuras en España y en Europa es ya tal, que es difícil o incluso imposible para algunas especies discernir entre zonas de efecto y zonas control. Como ecólogos, este es un conflicto de gran trascendencia en el que tenemos que tomar partido y dar respuestas con la mejor evidencia disponible y aplicando el principio de precaución, incluso si las respuestas no son al nivel de detalle que desearíamos o tienen una incertidumbre con la que no terminamos de sentirnos cómodos. En este sentido, en el Capítulo 2 se propone que una vía de avance sería la cuantificación a gran escala (regional o incluso nacional) del área de influencia de infraestructuras para aves y mamíferos, basándose en los resultados de un meta-análisis reciente (Benítez-López et al. 2010). Ya que las cuantificaciones derivadas de nuestra aproximación dependen del meta-análisis y éste tiene una serie de limitaciones, planteamos una estrategia para actualización y optimización continuada. A pesar de sus limitaciones, la aproximación que se propone tiene el potencial de ser una herramienta seria de gran utilidad en la conservación, planificación y gestión, mejorando (i) las estimaciones de la huella de infraestructuras o el mapeo de zonas silvestres (*wilderness areas*), (ii) la definición de zonas libres de carreteras (*roadless areas*) y (iii) las proyecciones a futuro de la influencia humana en la biodiversidad y el paisaje bajo varios escenarios alternativos.

Interacción entre los patrones espaciales resultantes de distintos procesos de cambio

En la literatura se asume comúnmente que existe una alta correlación entre los patrones de paisaje resultantes de distintas actividades humanas. Por ejemplo, se espera que las zonas con mayor dispersión urbanística tengan un desarrollo mayor de infraestructuras y, por tanto, valores más elevados de fragmentación del territorio (Theobald et al. 1997; Hawbaker et al. 2006). En este sentido, el mapa de proximidad a infraestructuras de transporte para toda Europa que se presenta en el Capítulo 2 guarda gran similitud con otros mapas de fragmentación del paisaje, dispersión urbanística y zonas de mínimo impacto humano publicados previamente (EEA & FOEN 2011; Ceaușu et al. 2015; Hennig et al. 2015).

En el Capítulo 3 se aborda esta interacción en profundidad. Si realmente los patrones de fragmentación de paisaje y dispersión urbanística son tan redundantes, podría reducirse el número de indicadores empleados en sistemas de seguimiento de objetivos de desarrollo sostenible, que son de más fácil aplicación cuanto menor sea el número de indicadores. De forma similar, cuando se aborda el estudio de los efectos de estos patrones en las comunidades bióticas, un menor número de variables predictoras permitiría simplificar el modelo de estudio. Sin embargo, los resultados del Capítulo 3 demuestran que esta alta redundancia no existe, o solo existe en algunas zonas, pero desde luego no predomina. Esta discordancia entre patrones de fragmentación de paisaje y de dispersión urbanística es la regla en vez de la excepción, en contra de lo esperado (Theobald et al. 1997; Hawbaker et al. 2006; Inostroza et al. 2013). La correlación entre dichos patrones varía especialmente de forma notable, así como a través de las distintas escalas estudiadas, siendo la correlación más alta a escalas más amplias. Por tanto, en el Capítulo 4 se han podido seleccionar paisajes con alta y baja congruencia de estos patrones. Como resultado, en la muestra de paisajes la correlación entre dispersión urbanística y fragmentación de paisaje es muy baja (1956: $r_p = 0.259$; 1980: $r_p = 0.046$; 2001: $r_p = 0.039$).

Los procesos de fragmentación de paisaje y dispersión urbanística no difieren solo en los patrones espaciales, sino que además se ha comprobado en el Capítulo 4 que ambos procesos afectan a las comunidades de aves asociadas a medios agrícolas de forma diferente. Mientras que el proceso de dispersión urbanística influye de forma negativa sobre la riqueza de aves, la fragmentación de paisaje repercute de forma negativa sobre el nivel de especialización de las comunidades. Por tanto, paisajes con niveles elevados de dispersión urbanística presentan menor riqueza de especies, mientras que paisajes con una elevada fragmentación tienen una mayor proporción de especies generalistas en cuanto a su preferencia de hábitat. Como conclusión, los indicadores de dispersión urbanística no son buenos sustitutos de los indicadores de fragmentación de paisaje y no se puede asumir que los efectos negativos derivados de ambos procesos vayan a ser similares.

Retraso de la respuesta de las aves de paisajes agrícolas mediterráneos a los cambios ambientales

Los paisajes agrícolas de la península Ibérica han sufrido profundos procesos de cambio, tanto de su estructura como de las condiciones climáticas a las que han estado sometidos desde mediados del s. XX, como mostramos en el Capítulo 4. Estos procesos han afectado a las comunidades de aves de estos medios (Robinson & Sutherland 2002; SEO/BirdLife 2012). Sin embargo, el hecho de que niveles actuales de riqueza se expliquen mejor por predictores ambientales de 1956 que por predictores actuales evidencia que las especies no están en equilibrio ni con el paisaje ni con el clima. Es decir, las especies no han respondido de forma inmediata a estos cambios, sino que exhiben un retraso en la respuesta. Este resultado es respaldado por los resultados inter-específicos, que indican que la distribución actual de la mayor parte de las aves consideradas se explica mejor con predictores ambientales del pasado.

El hecho de que múltiples procesos de cambio estén operando a la vez en el paisaje podría reducir capacidad de respuesta a estos cambios (Brook et al. 2008). El retraso en la respuesta de las especies sugiere la existencia de una *deuda de extinción* (Dullinger et al. 2013). Por tanto, las decisiones en materia de conservación tomadas basándose en cómo responden las aves de medios agrícolas a predictores actuales de paisaje pueden ser insuficientes para prevenir la pérdida de especies en el futuro (Kuussaari et al. 2009). Los paisajes que presenten una deuda de extinción mayor deberían ser identificados y convertirse en una prioridad de conservación para prevenir impactos adicionales, reforzar las poblaciones remanentes y restaurar interacciones y procesos ecológicos.

Paisajes agrícolas, incluso más complejos

En esta tesis se pone de manifiesto la extensa complejidad de los paisajes agrícolas. Los paisajes agrícolas de la cuenca mediterránea son altamente complejos, en términos de su variabilidad espacial y su variabilidad temporal (Benton et al. 2003). Sin embargo, al menos desde mediados del s. XX (aunque posiblemente antes) el patrón de desarrollo urbano y el desarrollo de vías de transporte también han moldeado las comunidades de aves. En el Capítulo 1 se empieza a apreciar la relevancia que la construcción de carreteras podía llegar a tener. Eso nos indujo a cuantificar la proximidad a infraestructuras en España y en toda Europa en el Capítulo 2. Los resultados evidenciaron la enorme contribución negativa que estas infraestructuras podían llegar a tener para la fauna en España y, en particular, para la fauna asociada a medios agrícolas. A pesar de ello, las consecuencias negativas de la influencia de infraestructuras son difíciles de calcular con precisión, ya que pueden amplificar los efectos de otros procesos de cambio como la intensificación agrícola o el cambio climático (Brook et al. 2008). Para mejorar el conocimiento y establecer relaciones generales entre la respuesta de las comunidades de aves y los procesos de cambio se requería una perspectiva de paisaje (Tscharntke et al. 2005).

En el capítulo 4 concluimos que la distribución de las aves asociadas a medios agrícolas es un fenómeno multifactorial determinado por la interacción de variables ambientales de paisaje y climáticas, cuya importancia relativa varía con el tipo de respuesta de la comunidad. Frente a la intensificación agrícola, a escala de paisaje destacan el patrón de dispersión de la urbanización y la temperatura como determinantes de la riqueza de especies. Considerando que alrededor de la mitad de todas las especies de Europa dependen de los paisajes agrícolas y que las aves agroesteparias son el grupo de aves más amenazado (PECBMS 2009), estos resultados deben ser considerados en sus estrategias de conservación.

Aunque esta tesis pone el centro de atención en los paisajes agrícolas de la cuenca mediterránea, los procesos que estudiamos – intensificación agrícola, desarrollo de infraestructuras de transporte, dispersión urbanística y cambio climático – tienen envergadura global, y afectan tanto a los países desarrollados como en desarrollo (Dulac 2013; Laurance et al. 2014). La investigación desarrollada en esta tesis doctoral tiene potencial para ser de gran relevancia para la ecología de paisaje, la biología de la conservación y otras disciplinas relacionadas. Además, ha conducido a una mejora del conocimiento de (i) las relaciones teóricas y empíricas entre procesos de cambios en el paisaje a múltiples escalas y (ii) los efectos del desarrollo de infraestructuras y actividades humanas en las poblaciones de fauna silvestre. Este conocimiento es fundamental para influir en la toma de decisiones en políticas de gestión y conservación.

Perspectivas

En los próximos años vamos a ver como convergen varios desafíos: el crecimiento poblacional, el crecimiento en el consumo de recursos y los cambios ambientales (Haber 2007). Estos procesos incrementarán la presión sobre los ecosistemas y harán las cosas muy difíciles, especialmente a través de una creciente competencia por el suelo (Foley et al. 2005; Haber 2007). Prueba de ello son los proyecto de creación de suelo ('land creation') del gobierno de China (Peiyue et al. 2014), que consisten básicamente en demoler montañas para promover el desarrollo, o el hecho de que se estén empezando a medir los efectos de la dispersión urbanística en el mar (*marine urban sprawl*; Dafforn et al. 2015).

Esta tesis pone de manifiesto la relevancia de la planificación espacial de este recurso para lograr mayores niveles de eficiencia en su consumo (y en el de otros recursos) y reducir los impactos de su utilización sobre la biodiversidad. Se hace por tanto necesario sugerir nuevas formas de diseñar, planificar y controlar que se haga un uso eficiente y responsable del suelo (EEA 2006; EEA & FOEN 2011) y, en definitiva, de nuestros paisajes. En relación a los procesos de fragmentación del paisaje por la expansión de infraestructuras y la dispersión de la urbanización, la prioridad es limitar ambos procesos por sus efectos ecológicos, algunos de los cuales se han presentado en esta tesis (Capítulos 1, 2 y 4). En casos en los que nuevos desarrollos estén justificados, es posible reducir los efectos ecológicos de ambos procesos mediante la implementación de estrategias de conservación para el desarrollo (*Conservation development*; Milder 2007; Pejchar et al. 2007)(medidas *a priori*) y la aplicación de medidas de defragmentación (van der Grift & Pouwels 2006) (medidas *a posteriori*). Estrategias como la conservación para el desarrollo, que tiene una implantación reducida en Europa, van más allá de la ciudad compacta (OECD 2012), integrando la conservación de la biodiversidad y los servicios ecosistémicos con el desarrollo.

Líneas de investigación futura

A partir de los resultados de esta tesis, sugerimos desarrollos en las siguientes líneas de investigación:

- Incrementar los esfuerzos para la cuantificación del área de influencia de infraestructuras para aves, mamíferos y otros taxones, mediante actualizaciones y mejoras del meta-análisis de Benítez-López et al. (2010) que es la referencia de nuestra propuesta metodológica. Para obtener resultados mejores y de mayor aplicación es imprescindible (i) realizar estudios empíricos más allá de Europa y Norteamérica, (ii) cuantificar distancias de efecto a otras infraestructuras que no sean carreteras (iii) y aumentar las investigaciones sobre los mecanismos que amplían o estrechan el área de influencia. Es recomendable que los nuevos estudios apliquen diseños de alta potencia inferencial, como diseños BACI y aproximaciones multi-escalares.

- A nivel de especie, se necesitan estudios comparativos para investigar como varía el tiempo de respuesta a los cambios ambientales entre especies o grupos de especies con distintos rasgos funcionales y proximidad filogenética, prestando una atención especial a la historia natural de las especies. Además, investigar el peso relativo que tienen los distintos procesos de cambio para cada especie sería de gran utilidad para mejorar sus estrategias de conservación.

- Identificar las zonas susceptibles de tener una alta deuda de extinción para aplicar medidas de gestión y conservación que eviten que la deuda de extinción se pague.

- Comprobar si las respuestas de las aves reproductoras son similares a la respuesta de las aves invernantes.

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Conclusions

1 Highway construction has detrimental effects on Great bustard populations via modified space use patterns and declining population trends. The avoidance behavior becomes evident from the beginning of the construction and once the highway is fully operational bustard numbers declined gradually.

2 The imprint of infrastructure extends over most of the country (55.5% in the case of birds, and 97.9% in mammals), predicting moderate declines in birds and severe declines in mammals. Farmland is the habitat most affected by transport infrastructure and built-up areas.

3 Researchers may no longer be able to measure the whole extent of the road effects on wide-ranging mammals and birds with large effect-distances in Spain, since core areas of significant size that could be used as controls are now almost inexistent, and this extends to most of Europe.

4 The approach we present to estimate the area of influence of infrastructure represents an important step forward for assessing the spatial extent of the impacts from infrastructure on bird and mammal populations at large-scales. The method proposed would benefit from reducing the spatial bias and incorporating new species' data sets.

5 The relationship between urban sprawl and landscape fragmentation patterns does not prevail. It is non-stationary, and scale-dependent. The spatial mismatches provide windows of opportunity for conservation through better development strategies.

6 Current diversity of farmland breeding birds in Mediterranean landscapes is not in equilibrium with current landscape structure and climate. It exhibits time-lagged responses of at least 20 years.

7 The relative importance of different environmental factors on the farmland bird communities depends on the type of response. Urban sprawl and climate change affect species richness, whereas agricultural intensification and landscape fragmentation influence the habitat breadth.

Conclusiones

1 La construcción de autopistas tiene efectos negativos en las poblaciones de avutardas al modificar los patrones de uso del espacio y al estar ligada a declives poblacionales. El comportamiento elusivo se hace evidente desde el inicio de la construcción y una vez la autopista se encuentra operativa, la tendencia poblacional diminuye gradualmente.

2 La huella de las infraestructuras se extiende a lo largo de la mayor parte del territorio (un 55.5% en el caso de las aves, y un 97.9% en en el caso de los mamíferos), prediciendo un descenso moderado en las aves y un declive severo en mamíferos. Las zonas de cultivo son el tipo de hábitat más afectado por las infraestructuras de transporte y las edificaciones.

3 Los investigadores podrían no ser ya capaces de medir los efectos de las carreteras en toda su extensión en mamíferos y aves con grandes distancias de efecto en España, ya que prácticamente no quedan areas de suficiente extensión disponibles para servir de control. Esta conclusión también es aplicable a la mayor parte de Europa.

4 Nuestro enfoque para estimar el área de influencia de las infraestructuras representa un paso importante para evaluar de la extensión espacial de los impactos de infraestructuras en poblaciones de aves y mamíferos. El método propuesto se beneficiaría de una reducción del sesgo espacial y de la incorporación de nuevas bases de datos de especies.

5 La relación entre la dispersión urbanística y los patrones de fragmentación del paisaje no es predominante, varía espacialmente y depende de la escala. Estas discordancias espaciales abren espacios de oportunidad para la conservación mediante mejores estrategias de desarrollo.

6 La actual diversidad de aves reproductoras de paisajes agrícolas mediterráneos no está en equilibrio con la estructura del paisaje ni con el clima actual. Ésta exhibe un retraso en la respuesta de al menos 20 años.

7 La importancia relativa de los distintos factores ambientales en las comunidades de aves de paisajes agrícolas depende del tipo de respuesta. La dispersión urbanística y el cambio climático afectan a la riqueza de especies, mientras que la intensificación agrícola y la fragmentación del paisaje influyen sobre la amplitud de hábitat de la comunidad.

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pero termina, sin duda, en el más especial de todos.

Castillejo de la Sierra (Cuenca)

En memoria de mi madre,
sus hermanos y mi abuela Eulalia.